THE DEMOGRAPHY AND INTERACTIONS OF *ECKLONIA RADIATA* IN SOUTHERN NEW ZEALAND

A thesis

submitted to the

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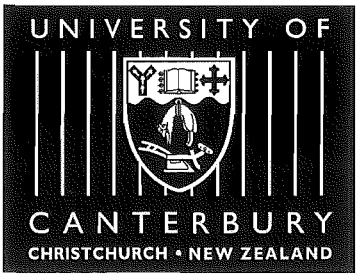
for the degree of

Doctor of Philosophy

by

Howard Royston Lees



2001

- Not an herb which carpeted the ground, not a branch which clothed the trees, was either broken or bent, nor did they extend horizontally; all stretched up to the surface of the ocean. Not a filament, not a ribbon, however thin they might be, but kept as straight as a rod of iron. The fuci and llianas grew in rigid perpendicular lines, due to the density of the element which had produced them. Motionless yet, when bent to one side by the hand, they directly resumed their former position. Truly it was the region of perpendicularity! -

Jules Verne
Twenty Thousand Leagues Under the Sea
Chapter XVI – A Submarine Forest

Contents

List of Figures

List of Tables

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Abstract

A demographic and experimental study was conducted on the laminarian alga *Ecklonia radiata* (C. Ag) J. Agardh. near the limit of its range in southern New Zealand at sites in Akaroa Harbour, Banks Peninsula, and Tory Channel in the Marlborough Sounds. These populations of *Ecklonia* are unique; their occurrence is shallow, yet their light environment is poor due to the presence of a *Macrocystis* canopy. Growth was slow compared to northern New Zealand and Australian populations, and productivity was also much lower. Population dynamics were explored in terms of both plant age and plant size: plant survival was closely linked to plant age, sori area was closely linked to plant biomass.

Significant morphological variation was found at scales of 3km within Akaroa Harbour, and scales of 300km between Akaroa Harbour and Tory Channel. *Ecklonia* in Ohinepaka Bay (Akaroa Harbour) had the longest stipes and greatest biomass of any site. Tory Channel plants had shorter stipes and longer lamina compared to plants from Akaroa Harbour. These morphological differences are discussed in relation to environmental differences between sites.

Orthogonal *Ecklonia* and *Macrocystis* manipulations tested the effect of both canopies on juvenile recruitment and growth. Canopy removal did not affect the recruitment of laminarians, but appeared to enhance survival of pre-existing recruits. Growth of understorey *E. radiata* generally increased following the removal of overlying canopy layers, but this was tempered by a high rate of lamina erosion in treatments where both canopies were removed. This was hypothesised to be a result of increased sedimentation in these treatments.

Dense stands of juvenile *E. radiata* were examined in relation to models of density dependent regulation. Findings suggest that plants do not experience large density effects, but these may become more severe as stands mature.

The effect of herbivorous invertebrate abundance was investigated in relation to macroalgal recruitment. Enclosure/exclosure cages suggested that an abundant and large herbivorous gastropod (*Cookia sulcata*) enhanced the recruitment and growth of macroalgae, possibly through consumption or redistribution of sediment.

The main finding of this study were that these southern New Zealand populations of *E. radiata* have constrained life-history characteristics. This limitation is mainly through growth suppression of recruits by overlying canopies, but the interactive effects of other factors, such as grazers, sediment, and larger-scale hydrodynamic processes cannot be discounted.

Chapter 1: General Introduction

1.1 General Introduction to Thesis

This thesis is a study of the demography and interactions of the subtidal kelp *Ecklonia radiata* near the limit of its range in southern New Zealand. Specifically, it deals with the response of *Ecklonia* to the low light environment within shallow *Macrocystis pyrifera* forests.

More generally, this thesis examines some of the factors that structure kelp communities. The ecology of subtidal marine algae has only been studied extensively since the development of SCUBA, over the past 50 years a picture has developed of the important factors that determine their distribution and abundance. The phycological literature is broadly divisible into physiological studies that examine the distribution and abundance of algae in relation to the constraints imposed by abiotic factors such as light, depth, temperature, nutrients, desiccation, exposure, and sedimentation (e.g. Gerard, 1984, 1997; Kain, 1966; Kennelly, 1989; Kirkman, 1989, Novaczek, 1984a, 1984b, 1984c; Salles *et al*, 1996; Bolton & Levitt, 1985; Hay, 1990; North & Zimmerman, 1984; Druel, 1984; Jackson, 1977; Peckol *et al* 1988; Airoldi, 1998), and studies that relate the distribution and abundance of algae to biotic interactions within and between species, such as life-history, competition, grazing, and predation (e.g. Reed & Foster, 1984; Dean *et al*, 1989; Worm & Chapman; 1996; Foster, 1982; Foster 1975a; Ayling, 1981; Lubchenco, 1980) (For review see Dayton, 1985; Schiel & Foster, 1986).

Historically, there has been vigorous debate concerning the relative importance of biotic and abiotic factors in determining the structure of macroalgal communities (Breen, 1987; Breen & Mann, 1976a, 1976b; Miller, 1985, 1987; Foster & Schiel, 1987). Recently, it has been recognised that the relative importance of these factors is scale dependent, and reliant on the questions being asked (Connell & Sousa, 1983; Dayton *et al*, 1998, 1999; Foster, 1990, Kennelly & Underwood, 1992). Biological factors, such as grazing, predation, competition and dispersal, are thought to predominate at smaller scales, while physical factors (light, temperature, nutrients, etc) operate at larger scales (Leonard, 1994). However, within this broad generalisation the question of how factors interrelate is possibly more important (Schiel & Foster, 1986; Lee & Brinkhuis, 1988). For example, light decreases with depth in subtidal habitats, but numerous other physical factors also vary with depth, such as temperature, water motion, nutrients and turbidity. Often the effect of one cannot be separated from the effect of another in any meaningful way.

Kelp forests are subtidally ubiquitous on rocky coastlines in temperate latitudes and are characterised by their vertical structure, usually consisting of different strata occupied by different algal guilds. Commonly, there is a surface canopy, consisting of buoyant fronds, an understorey of smaller, often stipitate kelps, and an encrusting and turfing community at the substratum. These kelp canopies exaggerate the effects of light attenuation in seawater (Graham, 1996; Gerard, 1984); dense surface canopies pre-empt a large proportion of available light and drastically reduce the amount reaching subcanopy layers (Maegawa *et al*, 1987). Gerard (1984) found that light levels at 4m beneath a *Macrocystis pyrifera* canopy were ~10% of those found at the surface. In the absence of a canopy light levels were ~30-80% of those found at the surface. Thus, kelp communities are very light limited environments (Reed & Foster, 1984), and this has consequences for the growth and recruitment of understorey species, as well as for the propagules of canopy forming species (Reed & Foster, 1984; Kimura & Foster, 1984; Chapman, 1984; Santelices & Ojeda, 1984; Novaczek, 1984a).

In addition to surface canopies, understorey canopies can also have large effects on algal recruitment and growth. This has been clearly demonstrated in the *Macrocystis* dominated kelp forests of California; removal of *Pterygophora californica*, the dominant understorey alga, resulted in an immediate recruitment of *M. pyrifera* and *P. californica* into cleared areas (Reed & Foster, 1984). The lowest strata within the kelp forest can also have a significant effect on community structure. Chapman (1984) showed that the recruitment of visible *Laminaria longicruris* sporophytes in Nova Scotia was enhanced ten-fold by the removal of red algal turf. Kennelly (1987a) experimentally removed dictyotalean turfing algae from an *E. radiata* bed in New South Wales and found that due to a residual turf effect, removal of this turf did not facilitate the recruitment of *Ecklonia* and the turf was able to return. However, subsequent studies demonstrated that the timing of disturbance was also important (Kennelly, 1987b). *Ecklonia* canopies cleared during spring, summer, and autumn resulted in a turf that persisted and inhibited *Ecklonia* recruitment for two years. Winter clearances during the period of densest kelp recruitment enabled *Ecklonia* to colonise alongside the turf, eventually shading and excluding it. Thus, biotic processes can also be important determinants of the outcome of successional processes within kelp forests (Foster, 1975a).

The persistence of kelp forest communities has been linked to low levels of physical disturbance (Kennelly, 1987c). In California, the persistence of the *Macrocystis* canopy is

closely linked to hydrological conditions, and this indirectly influences reproductive and recruitment schedules throughout the whole forest (Carr, 1989). Menge & Sutherland (1976) summarised the role of disturbance in marine communities; in habitats with benign physical environments, predation or grazing (biological disturbance) are major determinants of community structure. As harshness increases, and resources become limiting, (e.g. space, light, nutrients) competitive interactions between species will predominate. As environmental harshness increases further, species tolerance of physical disturbance will determine their persistence in communities. Biotic factors, such as grazing and competition, can influence kelp communities by acting either directly on algal species, or indirectly on the organisms that interact with algal species (Dean *et al*, 1989; Fletcher, 1987). Grazing plays an important role in determining community structure in areas with low levels of physical disturbance by regulating algal abundance and indirectly altering competitive interactions (Ebeling *et al*, 1985, Dayton *et al*, 1992). Natural or artificial reductions in grazer densities have led to increased algal abundance and changes in species composition (Reed & Foster, 1984).

The goal of demographic studies is to reveal the important aspects of a specie's life history and place these into a wider ecological context. Consequently, the aim of the present study was to describe the demography of *Ecklonia radiata* in relation to the low-light environment within sheltered *Macrocystis* dominated kelp forests in southern New Zealand. This study also examines the interactions of *Ecklonia* with the *Macrocystis* canopy, in relation to the effects of canopy shading and suppression, and the relationship between *Ecklonia* and the grazing invertebrate community. Canopy manipulations, and grazer exclusion/inclusion treatments, are the main experimental tools used.

Expectations of community structure in poorly studied ecological systems are often based on generalities formulated in analogous or homologous communities (Beck, 1997). However, considerable doubt has been placed on assumptions of habitat similarity between geographically distinct locales, especially in relation to subtidal assemblages (Foster, 1990). Processes shaping subtidal community structure in southern New Zealand may be quite distinct from those in superficially similar habitats in California (*M. pyrifera* and *Pterygophora californica* dominated forests) and Australia (*E. radiata* dominated kelp beds). Thus a wider aspect of this study will be to determine if general theories of sub-tidal community structure are broadly applicable to the kelp forests of southern New Zealand.

1.2 Thesis Outline

This thesis is divided into 6 chapters; the first and the last chapters are the General Introduction and the General Discussion respectively. The middle four chapters comprise the experimental and sampling portions of this thesis:-

Chapter 2 examines the demographic traits (growth, productivity, survivorship, reproduction, and recruitment) of *E. radiata* near the limit of its distribution in a shallow low light environment, and compares these traits with populations in open, unshaded habitats. This chapter poses the question: What effect does the highly turbid, low light environment of Akaroa Harbour have on the demographic parameters of *E. radiata*? The influences of age- and size-related traits on population demographics are also investigated.

Chapter 3 deals with a series of *Macrocystis* and *Ecklonia* canopy removal experiments. The question asked here was; Do these mature canopies limit the growth and recruitment of *E. radiata* (e.g. through light reduction and pre-emption of space) and is this effect homologous to that found in multi-tiered kelp communities elsewhere?

Chapter 4 examines the extent of intraspecific effects within relatively dense stands of juvenile *E. radiata* in relation to several general theories concerning density dependent regulation of growth and mortality.

Chapter 5 examines the distribution and abundance of herbivorous macroinvertebrates in Akaroa Harbour in relationship to macroalgal canopies, and focuses on the effect of a large herbivorous gastropod (*Cookia sulcata*) on recruitment.

1.3 Study Organism

Ecklonia radiata (C. Ag.) J. Agardh is a laminarian alga in the family Alariaceae. Mature plants consist of a single, solid erect stipe that is round or oval in cross section, arising from a holdfast with numerous branching haptera, and terminating in a strap-like primary lamina from which numerous secondary laminae arise (Schiel & Choat, 1980) (Figure 1). Between the top of the stipe and 10cm up the primary lamina lies the primary meristematic region, in which horizontal and vertical lamina expansion occurs (Kirkman, 1984). The primary lamina erodes at the distal end and is continuously replaced throughout life (Mann & Kirkman, 1981).

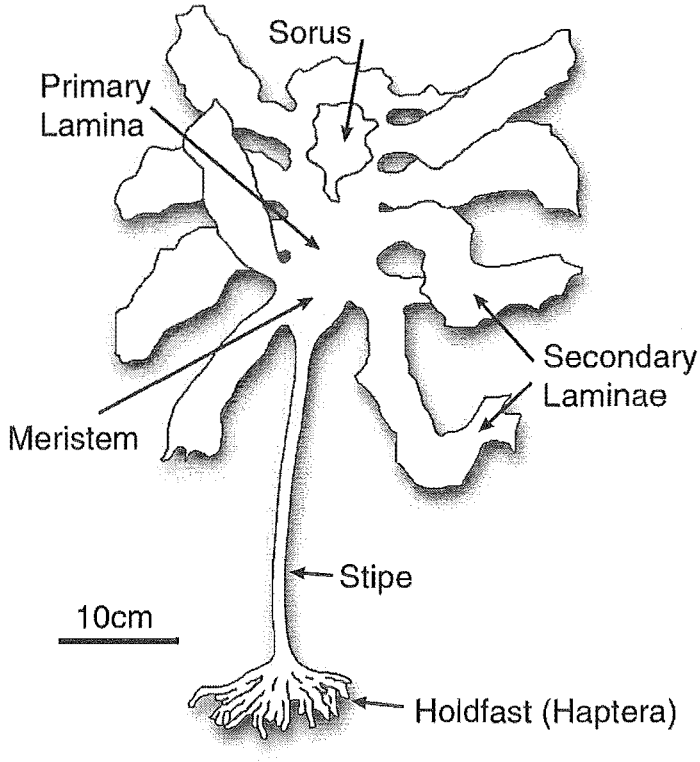

Figure 1. Diagrammatic representation of a mature *Ecklonia radiata*, with a morphology typical of the sites in this study. Redrawn from Adams (1994).

Ecklonia has a diphasic life history typical of laminarian algae. Zoosporangia within mucilaginous sori on the primary and secondary lamina release microscopic male and female zoospores that settle upon the substratum. These zoospores develop into male and female gametophytes up to 25μm in diameter. Upon maturity, female gametophytes release oogonia that are fertilised by male spermatozoids. Fertilised oogonia subsequently recruit as microscopic sporophytes (Jennings, 1967).

Sporophytes first become visible in the field as small blades 5-10mm in length. Initial growth occurs mainly through lamina elongation; beyond ~250mm secondary lamina are produced and the stipe begins to lengthen.

Ecklonia is excluded from the immediate subtidal by its inability to compete with fucoids, lack of tolerance to high wave action, or photosynthetic inhibition (Choat & Schiel, 1982). However, in clear waters it can extend from the sublittoral fringe to depths of 65m and may come to physically dominate large areas, providing food and habitat for large numbers of organisms (Novaczek, 1984c). It is also a major contributor to detritus based food webs because of constant frond erosion (Mann, 1973). Primary productivity within a kelp community may be as high as anywhere on Earth, up to 90% of which enters detritus-based food chains as POM or DOM (Mann 1973). *Ecklonia* is perennial and may live for up to ten years although a maximum of seven years is more common (Schiel & Choat, 1980; Novaczek, 1981). There is a large degree of morphological variation over its geographical distribution. Plants in New Zealand generally have longer stipes at maturity than Australian varieties, although short stiped (<20cm) plants are found in restricted localities and are regarded as environmentally induced (Larkum, 1986).

Ecklonia forms extensive subtidal forests in warm temperate waters of the Southern Hemisphere, extending as far south as the Snares Islands, and is the dominant algal species on the subtidal reefs of most of southern Australia (Womersley, 1981; Kirkman, 1984) and northern New Zealand (Schiel & Nelson, 1990). The distribution of *Ecklonia* overlaps with that of the giant kelp, *Macrocystis pyrifera*, in parts of the Indian Ocean, Tasmania, and southern New Zealand (Womersley, 1954). The distribution of *Macrocystis* within New Zealand is thought to correspond with the cool regions of the Southland current; where the maximum monthly mean temperature is less than 16-17°C (Hay, 1990). Hence, *Macrocystis* does not occur further north than Castle Point on the east coast of the North Island, or Jacksons Head on the west coast of the South Island (Hay, 1990). At sites where they co-occur, *Ecklonia* forms a subcanopy beneath a dominating *Macrocystis* canopy. This dominance is expressed in terms of biomass and the ability to pre-empt light with an extensive and dense surface canopy. The light environment beneath a *Macrocystis* canopy is highly variable, due to wave-induced movement of fronds that generate light-flecks (Wing, *et al,* 1993; Gerard, 1984). The morphology and demography of *Ecklonia* as an understorey species beneath the *Macrocystis* canopy has not been described previously.

1.4 Study Sites

The majority of the work in this thesis was carried out in two large *Macrocystis* dominated kelp forests: Wainui Bay and Ohinepaka Bay in Akaroa Harbour, Banks Peninsula. Additional sites were subsequently added at Cape Three Points in Akaroa Harbour, and at Tory Channel in the Marlborough Sounds (Figure 2).

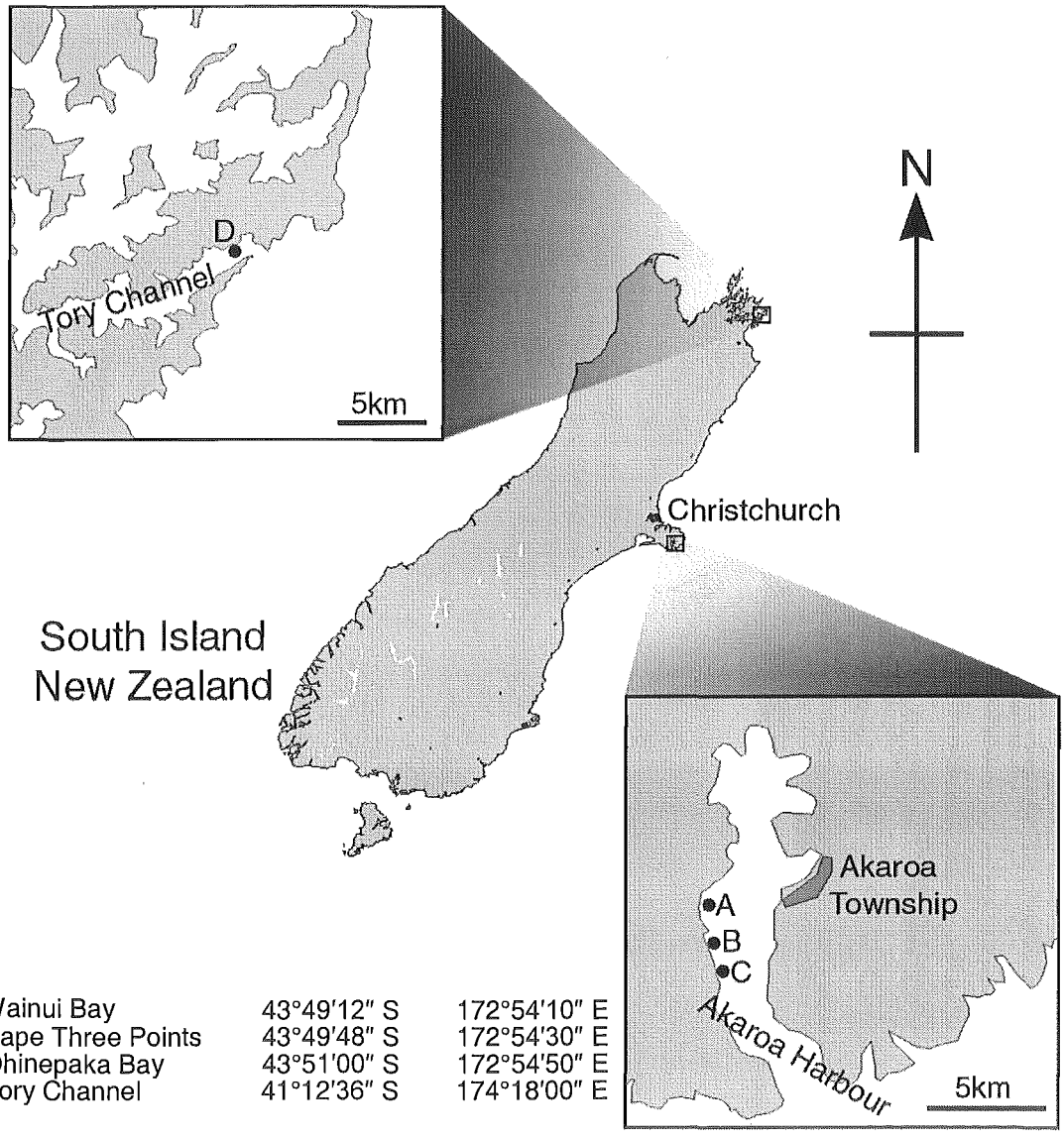

Figure 2. Location of study sites in the South Island of New Zealand. Three study sites were located in Akaroa Harbour on Banks Peninsula, the fourth site was located in Tory Channel, Marlborough Sounds.

Akaroa Harbour was formed by the collapse of the southern crater-wall of an extinct volcano, allowing seawater to enter. As a result, the harbour opens to the south and is subject to periodic southerly winds and oceanic swell. The surrounding hills are composed primarily of compacted loess. Following heavy rain, excessive runoff dramatically increases the

turbidity of coastal water for long periods (Plate 1). Kelp forests containing *Ecklonia radiata* and *Macrocystis pyrifera* are present subtidally in sheltered embayments with rocky substrata. The surface *Macrocystis* canopy varies greatly in extent through time (Figure 3). More exposed sites near the harbour entrance are dominated by *Durvillaea antarctica*. The kelp forest in Wainui Bay was the largest, measuring ~100 x 670m in area. The forest at Ohinepaka Bay measured ~300 x 50m, and at Cape Three Points ~80 x 300m (Figure 2).

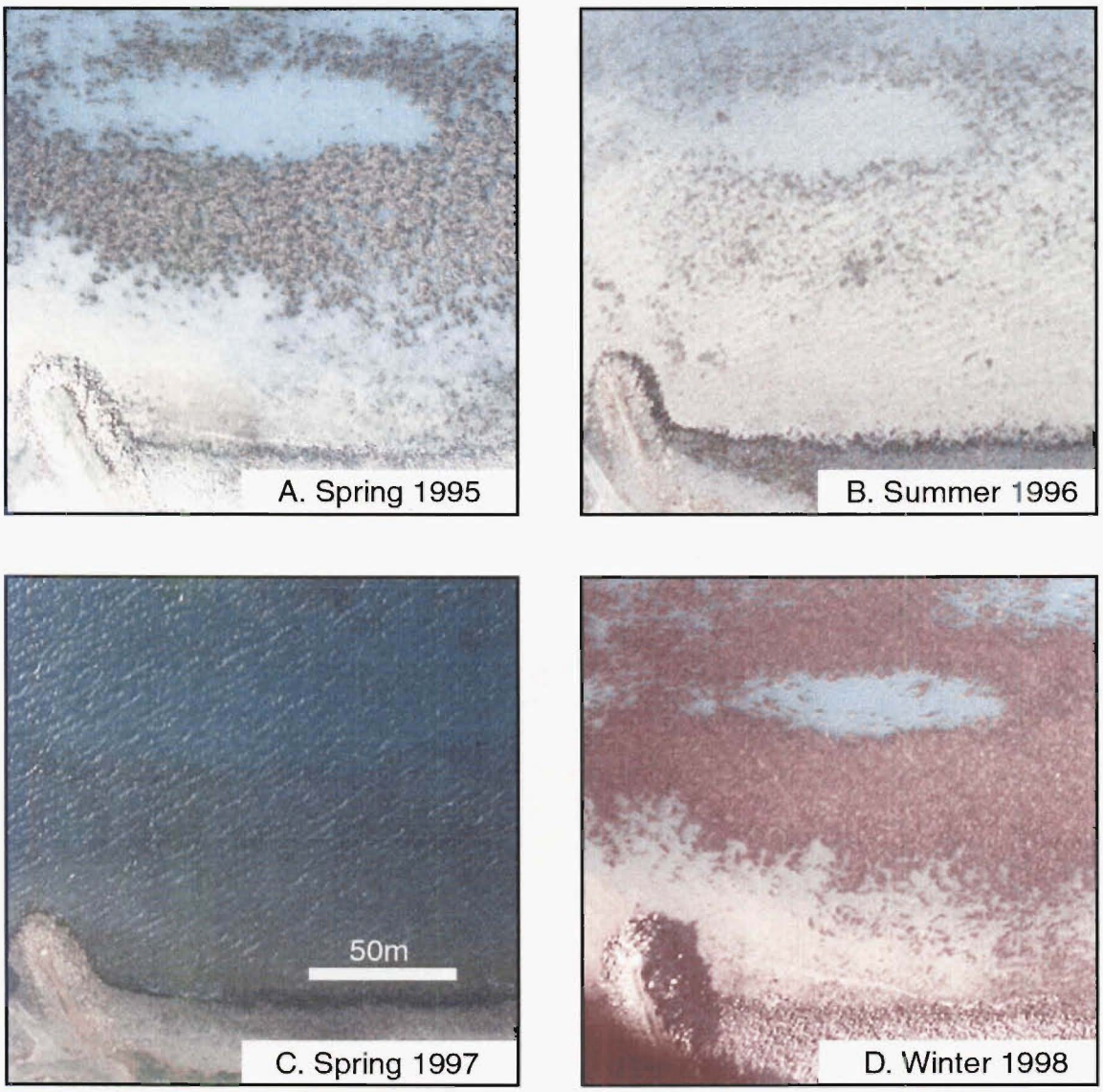

Figure 3 A-D. Aerial photographs of the Wainui Bay Kelp forest and the adjacent slipway and breakwater, showing variation in surface *Macrocystis* canopy through time. Photographs were all taken at low tide.

The Akaroa kelp forests extended from the immediate subtidal to depths of 4-5m at all sites. However, inshore areas were particularly turbid and subject to surge, so this study was confined to deeper regions below 3m. There are differences in substratum between sites, which determined the placement of some experiments. Wainui Bay generally consists of

igneous boulders up to 1m in diameter, the interstitial spaces of which are occupied by coarse sand and detritus. Cape Three Points and Ohinepaka Bay consist of an irregular reef composed of submerged clay. At all sites the primary substratum is covered with a layer of coralline algae (Plate 2).

An additional site was added in the Marlborough Sounds, adjacent to an abandoned Whaling Station near the eastern heads of Tory Channel. This site is hydrographically distinct from the Akaroa sites, tidal flow is quite strong, and the channel is regularly flushed with oceanic water, hence water clarity is much greater than at the Akaroa sites.

Attempts were made to quantify differences in water motion between Wainui Bay and Ohinepaka Bay using plaster-of-Paris spheres (Gerard & Mann, 1979), but these proved inconclusive. However, of the sites in Akaroa Harbour, Wainui Bay and Cape Three Points are probably more exposed than Ohinepaka Bay, as the former have direct line-of-sight to the harbour entrance and are thus directly exposed to strong southerly weather. The latter is sheltered by a prominent headland.

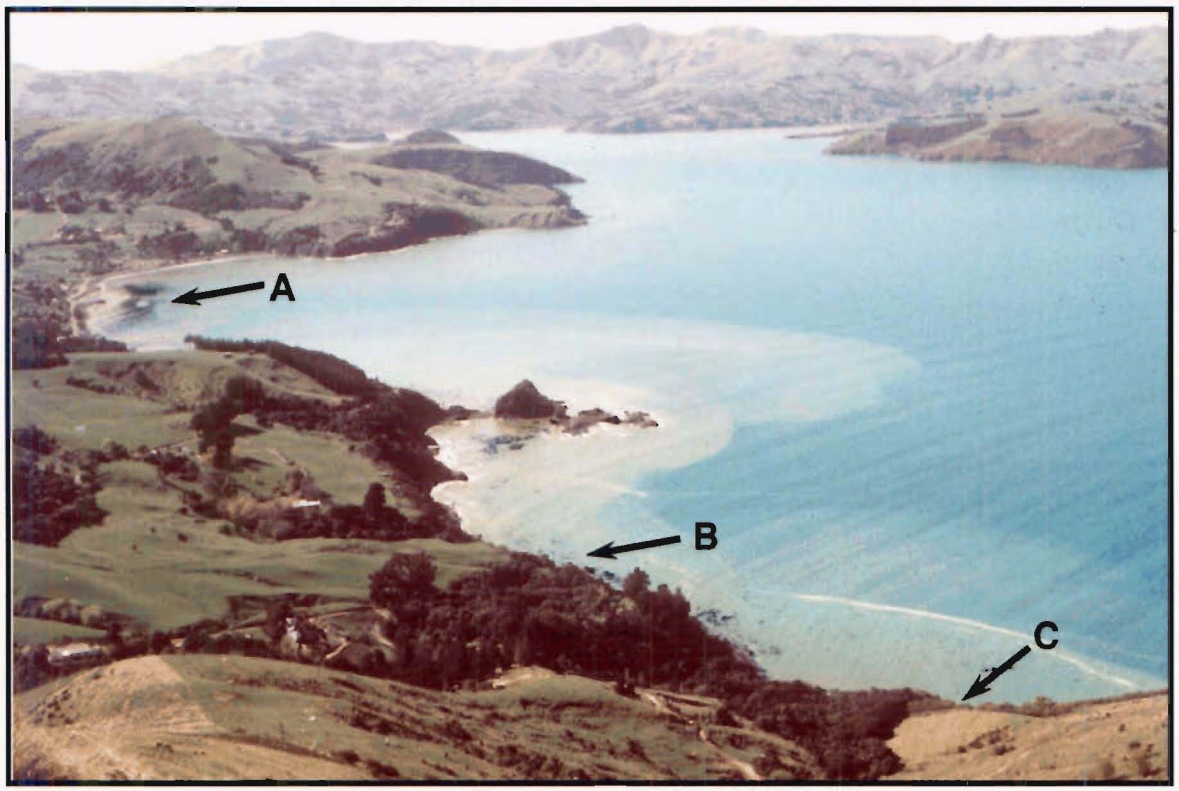

Plate 1. Land based photograph of Akaroa Harbour, Banks Peninsula, facing northeast. Arrows indicate locations of study sites. A = Wainui Bay, B = Cape Three Points, C = Ohinepaka Bay. Note turbidity of inshore areas (following rain), and ocean swell from the south.

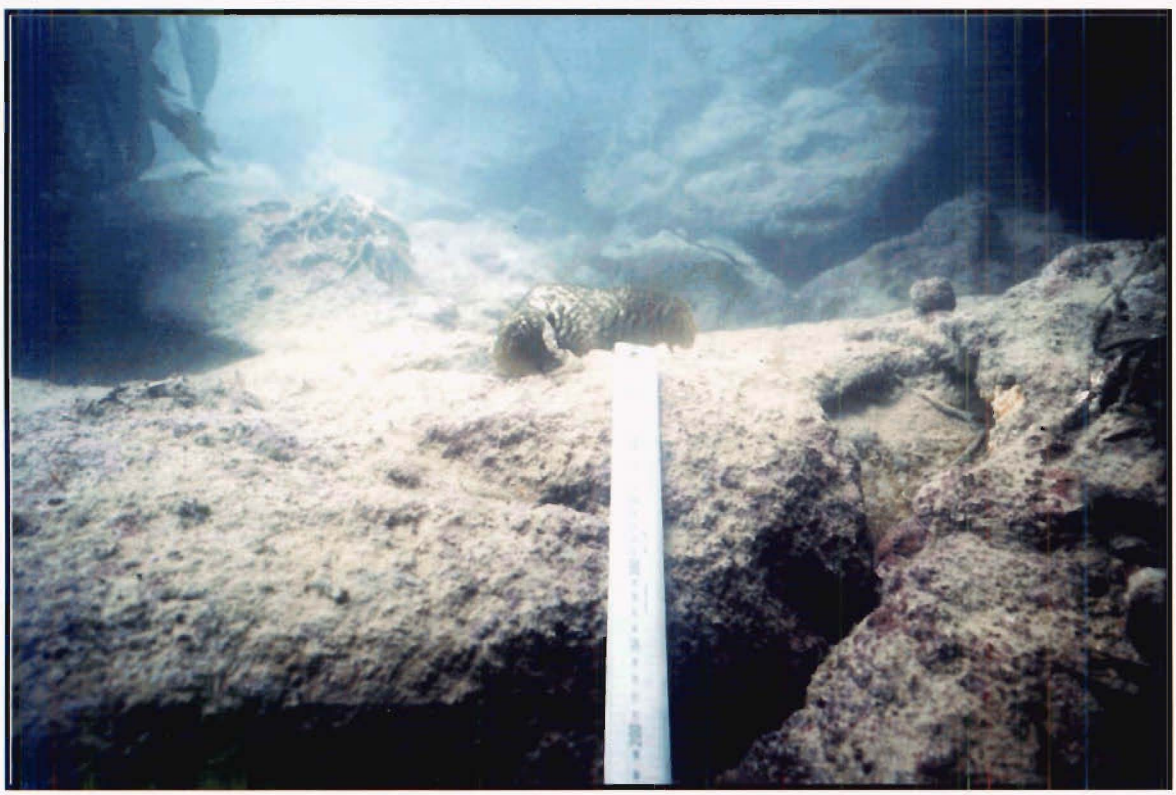

Plate 2. Typical substratum encountered in Akaroa Harbour kelp forests. The substratum is generally covered with encrusting coralline (*Litholamnion* spp.) and variable quantities of fine sediment. The solitary *E. radiata* juvenile in the centre of the photograph is ~150mm in length.

Chapter 2: General Demography

2.1 Introduction

The demography of northern New Zealand and Australian populations of *Ecklonia radiata* has been described by many authors (Novaczek, 1981, 1984c; Schiel, 1981, 1988; Choat & Schiel, 1982; Kirkman, 1981, 1984; Larkum, 1986; Hatcher *et al* 1987). The occurrence of *E. radiata* as an understorey species within the *Macrocystis pyrifera* forests of southern New Zealand is unique, yet its demography in this situation has not been described.

In recent years there has been a shift away from age-based algal demography in favour of size-based (or stage-based) methods (Chapman, 1986 1993; Ang & De Wreede, 1990; Ang, 1991; Russell, 1990). The use of size is warranted in many circumstances since algae generally exhibit a very plastic morphology and size is often more closely correlated to demographic events than plant age (Kirkpatrick, 1984; Ang & De Wreede, 1990; Chapman, 1995). For example, Chapman (1993) found that a life and fertility table generated from the age-specific survival and fecundity of *Laminaria digitata* did not produce accurate estimates of population growth. Size-based projection matrices did, however, produce population forecasts that agreed with empirical data. In addition, size-based demography more accurately reflects the effects of disturbances, such as herbivory (Andrew & Jones, 1990).

However, it is often important to also discern the age-structure of a population because this may provide insights into population dynamics that cannot be determined from size-structure alone (De Wreede, 1986; Cheshire & Hallam, 1989; Hymanson *et al*, 1990). Similarly, the significance of past events may often be readily interpreted from the age-structure of the present population. It is evident that certain demographic features, particularly survival, may be more dependent on age than size. Chapman (1986) found that mortality of *Laminaria longicruris* was more related to age than size. De Wreede (1986) found age-specific survivorship of *P. californica* to vary between populations. One population had a constant age-specific survivorship, but in another, younger plants had a higher mortality. The effects of age and/or size can be outweighed by seasonal variability; Ang (1991) found that the probability of mortality was not uniform for *Fucus distichus* of the same age/size at different times of the year.

Whether or not the demography of an algal species can best be described in terms of age or size is highly dependent on its morphology. For example, the intertidal alga *Ascophyllum nodosum* is best described in terms of size because large portions of the plant are often lost (Aberg, 1992a). *E. radiata,* as with most other laminarians, effectively consists of two portions, a perennial stipe and a lamina that is continually replaced throughout life. Loss or

damage of the stipe will generally result in death. Provided the primary meristem remains intact, lamina loss will only lead to plant mortality in extreme cases. Hence it is likely that mortality risk will be a function of stipe condition, and possibly age. Reproductive structures are borne on the lamina, so fecundity is likely to be size (biomass) dependent.

This study assesses the age- and size-structure of *E. radiata* populations in Akaroa Harbour. The objectives are twofold. The first is to provide a general description of populations of *E. radiata* in southern New Zealand, and compare estimates of growth rate, density, fecundity, morphology with studies on *E. radiata* elsewhere. The second is to use size- and age-based demographic techniques to examine overall population variables, such as stable size/age distribution and population growth rate. The supposition that demographic parameters of *E. radiata* are best considered in terms of age and size due to a mixture of annual and perennial morphology is also examined.

2.2 Methods

The methods fall into two broad categories: sampling methods used to obtain raw demographic data, and methods of data manipulation used in the derivation of age, biomass, fecundity, and the construction of transition matrices and life tables. These will be considered in turn.

2.2.1 Sampling Methods

2.2.1.1 Tagged plants

In July 1995, 100 *E. radiata* were tagged in Wainui Bay, Akaroa Harbour. In November 1995 a further 99 *E. radiata* were tagged at Ohinepaka Bay, also within Akaroa Harbour, but 3km south (Figure 2). An additional 60 plants were tagged in a kelp forest near the whaling station in Tory Channel at the north end of the South Island in March 1996 (Figure 2). Tags consisted of uniquely numbered DYMO™ tape strips threaded onto insulated ni-chrome wire, and then twisted loosely around the stipe of each *E. radiata* near the holdfast. Three parameters were measured on each tagged plant. 1) Stipe diameter, the widest diameter approximately 2 cm above the holdfast. 2) Stipe length, measured from the top of the holdfast to the base of the lamina. 3) Total length, measured from the top of the holdfast to the tip of the primary lamina (excluding secondary lamina). A broad size range of plants was tagged at each site (Table 1).

Table 1. Initial size range of *Ecklonia* tagged at three sites.

		Wainui Bay (n=100)	Ohinepaka Bay (n=99)	Tory Channel (n=60)
Total length	**- min**	100mm	75mm	200mm
	- max	1075mm	1100mm	1200mm
	- x ± 1 SE	504.6 ±19.1	384.2±21.0	636.2±24.1
Stipe length	**- min**	8mm	5mm	16mm
	- max	570mm	580mm	570mm
	- x ± 1 SE	179.4±14.6	115.9±17.17	166.2±17.4
Stipe diameter	**- min**	1mm	1mm	3.5mm
	- max	19mm	17mm	15.5mm
	- x ± 1 SE	10.3±0.4	6.4±0.5	10.8±0.4

Tagged *Ecklonia* in Wainui and Ohinepaka Bays were visited at approximately quarterly intervals for three years. On each visit, new plants were tagged to replace lost ones. Surviving plants at the Tory Channel site were re-sampled once in September 1998.

In addition to tagging relatively large plants, 26 newly recruited *E. radiata* (mean length 28.1mm ± 3.2mm SE) were mapped relative to epoxy markers in March 1997 following an extensive search of an area ~5m x 5m within the Wainui Bay kelp forest. At the Ohinepaka

Bay site, 61 newly recruited *E. radiata* were mapped and measured in March 1998 (mean length 27.0mm ± 2.6mm SE).

To assess gross lamina elongation and provide a rough estimate of plant productivity, a hole-punching technique was employed on approximately 25 plants in both Wainui and Ohinepaka Bays over the course of one year (Mann & Kirkman, 1981). A hole approximately 5mm in diameter was punched in the primary lamina 10cm above the junction with the stipe, in order to avoid the meristem. On subsequent visits the distance travelled by the hole was measured, and a new hole was punched.

2.2.1.2 Destructive Sampling

At approximately quarterly intervals, twenty *Ecklonia* within the Akaroa forests were randomly selected and removed. These samples were drained then measured (stipe diameter, stipe length, total length), then wet-weighed, then dried in an oven at ~60°C for 2 weeks before being weighed again. Subsequent samples were only measured and wet-weighed. Additional parameters were included in later samples to determine if they provided better predictors of biomass (they didn't). These were the stipe diameter midway up the stipe, holdfast diameter (max), and number of secondary lamina.

The presence or absence of reproductive structures (sori) was assessed on all destructively sampled plants. From November 1996 the sori area of mature plants was assessed (max length x max width of each sorus). Sori were subjectively categorised as either 'full' or 'spent' based on visual appearance. Full sori appeared darker than surrounding tissue when held up to the light, while spent sori appeared lighter than surrounding tissue. This method was validated by inducing spore release from both full and spent sori. Five full sori of known area were each partially dried and then flooded with 250ml of filtered seawater. The number of spores released per ml was estimated using a haemocytometer five times within each sample. This was then converted into spores.cm^{-2} of sori area.

In November 1995, 20 destructively sampled plants were examined for stipe growth rings using the methods of Novaczek (1981). In all plants of a variety of sizes (and presumably ages), no annual growth rings were detected. Subsequently, thirty tagged plants of known minimum age were destructively sampled in January 1999. As before, no stipe rings were visible that corresponded with the known ages of these plants.

2.2.1.3 Random Transects

To keep track of natural fluctuations in *Ecklonia* abundance and size structure, two random transects were performed at each site in Akaroa Harbour at approximately quarterly

intervals. A twenty-meter tape measure was laid haphazardly along the seafloor, and at five random intervals a $1m^2$ quadrat was laid out. All *Ecklonia* within the quadrats were measured for stipe diameter, stipe length, and total length.

2.2.1.4 Recruitment

The appearance of recruits was assessed within random transects (Section 2.2.1.3). To assess recruitment onto natural substrata, 5 concrete slabs measuring 19 x 19cm were placed at Ohinepaka Bay in winter 1997, and sampled frequently until spring 1998 for the appearance of recruits. Concrete blocks placed in Wainui Bay in winter 1997 as part of an investigation into the effects of grazers on algal recruitment (Chapter 5) were similarly sampled for recruits until spring 1998. It was noted that within the Wainui Bay kelp forest, recruits appeared to be more abundant on the intact holdfasts of dead adult plants than elsewhere. Stratified sampling of dead holdfasts with at least one visible recruit was begun in spring 1997 at the Wainui Bay site. Five holdfasts were carefully removed and the size, number, and species of recruits were assessed. Repeat sampling was performed every 1-2 months during the recruitment period. By April 1998, 25 holdfasts had been collected and holdfasts containing recruits had become scarce.

2.2.2 Derivations

2.2.2.1 Derivation of Ecklonia *Growth Rates*

The growth rate of tagged plants was defined as the net change in size per unit time. As a consequence, negative growth is possible, especially in relation to net lamina elongation, where erosion at the distal end may outpace production at the meristem. Similarly, stipe diameter and stipe length may appear to undergo negative growth when new haptera layers are produced above the holdfast. These new haptera layers effectively reduce stipe length, and also force stipe diameter to be measured further up the stipe where it may be narrower. In addition to net lamina elongation rate, which is a function of growth minus erosion, gross lamina elongation was measured by hole-punching ~25 plants at Wainui and Ohinepaka Bays (see section 2.2.1.1).

2.2.2.2 Derivation of Ecklonia *Age (non-destructive)*

Without following a cohort from recruitment to death, the age of larger *E. radiata* can only be estimated by examining perennial portions, such as the stipe and holdfast. Previous studies have attempted to use stipe growth rings in *E. radiata* and other stipitate kelps with little success (Novaczek, 1981; Larkum, 1986; De Wreede, 1986). Stipe growth rings are not a feature of *E. radiata* in Akaroa Harbour. To overcome this limitation some authors have

used physical size as a measure of age in seaweeds (De Wreede 1984, Hymanson *et al* 1990; Cheshire & Hallam, 1989). The stipe is a perennial portion of the plant that increases incrementally in size with time, thus stipe size was hypothesised to be a good estimate of age in *E. radiata*. Stipe size, in terms of biomass, was highly correlated with stipe volume at both Wainui ($r=.95$, $p<.01$) and Ohinepaka Bays ($r=.92$, $p<.01$). Thus stipe volume was used as a proxy for age. This also meant that plants could be measured in situ. Stipe volume was estimated by assuming that the stipe is a cylinder of uniform proportions (Equation 1) (Hayashida, 1984).

Equation 1. Calculation of *Ecklonia* stipe volume

$$\text{Stipe volume}\,(\text{cm}^3) = \pi \times \left(\frac{\text{Stipe diameter (cm)}}{2}\right)^2 \times \text{Stipe length (cm)}$$

To validate the use of stipe volume as a proxy for age, the growth in stipe-volume of tagged plants was used to construct a composite growth curve of age versus stipe-volume for both Akaroa sites (Figure 4). Stipe-volume (cm^3) was transformed to the cube of root stipe-volume (cm) for convenient division into 0.5cm initial size-categories. Data were fitted to the growth curve by assuming that plants in the smallest category (<0.5cm) were newly recruited y0 plants. The mean stipe-volume of these plants in successive years was used as the basis for categorising plants in larger initial size categories. For example, if the mean size of y0 plants at the end of one year was 1cm, then plants initially tagged at ~1cm were assumed to be y1 plants.

In this way a composite growth curve was built-up, encompassing the entire lifespan of a hypothetical *E. radiata* plant. It was assumed that plants of similar stipe-volume, but with different proportions of stipe-diameter and stipe-length, had the same mean stipe-volume growth rate. This is an important assumption because the progression of individuals from one age-class to the next requires that plants of initially similar stipe volume will have similar stipe-volume the next year, regardless of initial stipe proportions. Regression of growth rate against the ratio of stipe-diameter to stipe-length revealed significant relationships at both sites. Despite this, the low R^2 values obtained suggest that stipe-volume growth rate was essentially constant at all ratios of stipe-diameter to stipe-length (Wainui: $y=0.0027x + 0.0049$; $R^2=0.054$; $p<0.01$; $n=680$. Ohinepaka: $y=0.0024x + 0.0111$; $R^2=0.067$; $p<0.01$; $n=538$).

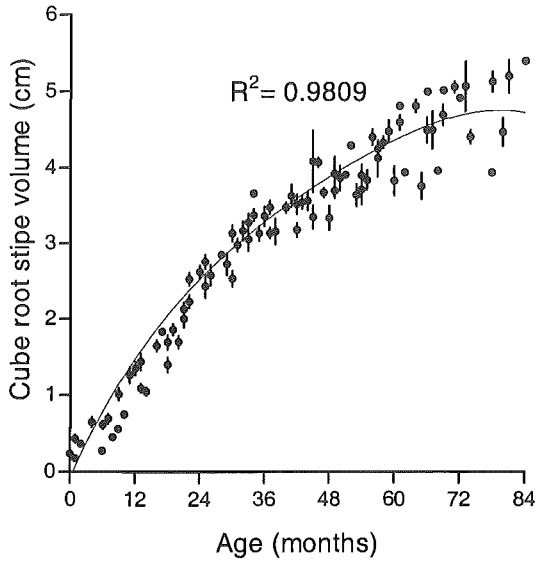

Figure 4. Composite stipe volume growth curve constructed from mean growth of tagged *E. radiata* in concurrent 3-year periods.

The limitations of this approach are that the final curve may be sensitive to the size of the arbitrarily chosen initial size categories and the numbers of plants within those categories. Additionally, natural size variability within each age group decreases the precision of individual estimates of age.

The growth curves constructed for Wainui and Ohinepaka Bays were not significantly different (Mann-Whitney t-test U= 989.0; p=0.6211), so their curves were pooled (Figure 4). From the resultant curve, age-specific stipe volumes were obtained (Table 2)

Table 2. Derivation of *E. radiata* age from stipe-volume measurements. Based on the polynomial equation $Y=A+(Bx)+(Cx^2)+(Dx^3)+(Ex^4)$, where A=-0.08247, B=0.1600, C=-0.002844, D=3.412 x 10^{-5}, E=-1.765 x 10^{-7}. R^2 = 0.98.

Estimated Age (years)	Cube-root stipe volume (cm)	Stipe volume (cm^3)
0 – 1	0.000 - 1.483	0.00 - 3.26
1 – 2	1.483 - 2.532	3.26 - 16.23
2 – 3	2.532 - 3.287	16.23 – 35.51
3 – 4	3.287 - 3.881	35.51 – 58.46
4 – 5	3.881 - 4.361	58.46 – 82.94
5 – 6	4.361 - 4.686	82.94 – 102.90
6 +	4.686 +	102.90 +

2.2.2.3 Derivation of Biomass (non-destructive)

The biomass of non-destructively sampled *Ecklonia* was estimated using morphometric data from destructively sampled plants. The best estimate of fresh *Ecklonia* biomass was determined to be a function based on transformed values of stipe diameter and lamina length (Equation 2).

Equation 2. Estimate of biomass determined by multiple regression

$$\textit{Ecklonia}\ \text{Biomass (g)} = ((\text{Stipe diameter(mm)}^2 \times A) + (\sqrt{\text{Lamina length (mm)}} \times B) + C)^3$$

Wainui Bay: A= 0.020, B= 0.130, C= 0.295 : R^2 = 0.81 n=96 p<0.01
Ohinepaka Bay: A= 0.017, B= 0.178, C= -0.064 : R^2 = 0.70 n=78 p<0.01

The benefit of using a function of stipe diameter and lamina length as an estimate of biomass is that it allows the construction of transition matrices that incorporate transitions from larger to smaller size classes. This is important because plants will often lose portions of their lamina, and consequently reduce in biomass.

2.2.2.4 Derivation of Reproductive Output

The construction of transition matrices and life tables requires that the reproductive contribution of each age/size class be known with some certainty. However, there are some inherent difficulties associated with the assessment of reproduction in laminarian algae, such as their diphasic life history consisting of both gametophyte and sporophyte generations, and the large number of microscopic offspring, which generally remain undetectable until quite late in their development. In regard to these difficulties, several assumptions were made in assessing details of *E. radiata* reproduction. First, it was assumed that the contribution of any mature *E. radiata* to the observed number of recruits is proportional to the reproductive area (total sori area) of that individual. It was also assumed that the sori area of a mature *E. radiata* is proportional to its biomass. Previous authors have used similar indirect methods of determining reproductive output. Aberg (1992b) assumed fertility to be proportional to reproductive biomass in *Ascophyllum nodosum*. Futhermore, Cheshire & Hallam (1989) used biomass as a measure of reproductive potential in *Durvillaea potatorum*. In a similar way, Ang & De Wreede (1990) assumed that the number of *Sargassum siliquosum* recruits per 0.25m^2 was a function of plant volume, which is allometrically related to plant length.

In all plants with sori, reproductive allocation was assumed to be independent of age. For the purposes of matrix construction, full and spent sori were regarded as equivalent.

2.2.2.5 Derivation of Productivity

Productivity of *E. radiata* at Wainui and Ohinepaka Bays was estimated from frond growth measurements obtained via hole-punching of tagged plants (see 2.2.1.1). The annual growth in millimetres was converted into wet-weight estimates of lamina biomass production, and then to dry-weight (lamina wet-dry: R^2 =0.92, p<0.01, n=22). Dry-weight

production of stipe biomass was estimated in a similar way from annual stipe volume growth rates (stipe wet-dry: R^2 =0.89, p<0.01, n=19). Productivity per m^2 was estimated using mean densities of *E. radiata* at each site and expressed as $g_{dry}.m^{-2}.yr^{-1}$. However, a point to note is that although similar methods were used to calculate productivity at both sites (measuring the distance travelled by a hole punched in the lamina), this does not account for variations in biomass distribution along the primary lamina, unless specifically calibrated (Mann & Kirkman, 1981).

2.2.2.6 Transition Matrices

The use of transition matrices, as well as life and fertility tables, has not been previously attempted for *E. radiata*. The estimated biomass of tagged plants was used to construct transition matrices for the Wainui and Ohinepaka Bay populations. Tagged plant data were divided into the following biomass categories:- <20g; 21-40g; 41-80g; 81-160g; 161-320g; 321-640g; 641-1280g; >1280g. The annual probability of transition from one size class to another was calculated for each size-class (biomass), based on the survival, growth, and erosion of tagged *E. radiata* over three one-year periods, 1995-96, 1996-97, and 1997-98. The transition probabilities were entered into a size-based projection matrix (Lefkovitch, 1965) of the form:-

$$\begin{bmatrix} P_1 & F_2 & F_3 & .. & F_n \\ G_{1,2} & P_2 & D_{3,2} & .. & D_{n,2} \\ G_{1,3} & G_{2,3} & P_3 & .. & D_{n,3} \\ .. & .. & .. & .. & D_{n,4} \\ G_{1,n} & G_{2,n}. & G_{3,n} & G_{4,n} & P_n \end{bmatrix}$$

Where P = the probability of survival within the same size class, G = probability of survival and growth to a larger size class, D= probability of survival and erosion to a smaller size class. F = the probability of survival and erosion from a larger size class to the smallest size class, and the contribution of larger size classes to recruitment of the smallest size class. Size-specific fecundity was estimated as a function of sori area and scaled in relation to observed recruits (see section 2.2.2.4).

The transition matrices were used to project the stable size distribution and also estimate the finite rate of increase (λ) of the *E. radiata* populations in Wainui and Ohinepaka Bays. Stable size-distributions were compared to actual distributions determined by random transect using single classification χ^2 (Chapman, 1993).

Lack of predictive power in matrix models can stem from several factors, such as high variability in size-specific survivorship (De Wreede, 1986) and environmental instability (Lefkovitch, 1965). Low predictive power is especially apparent in studies of marine algae. Difficulties involved in recognising very small recruits *in situ* can lead to an underestimation of their abundance. In this study, and in many others (Aberg, 1992a, 1992b; Cheshire & Hallam, 1989; Ang & De Wreede, 1990), the demography of early life-history stages (spores, gametophytes, early sporophytes) could not be analysed in detail. Fully predictive models will only be possible when all components of the life history are included, and when demographic data on all life history stages are obtained (De Wreede, 1986). Methods of obtaining such detailed information do not currently exist (Ang & De Wreede, 1990).

2.2.2.7 Life and Fertility Tables

Life and fertility tables were constructed for the Wainui and Ohinepaka Bay populations using the annual survival probabilities of tagged plants grouped by age (derived from stipe-volume). Assessment of age-specific reproduction was based on the minimum age at which sori were observed on plants. Beyond this minimum age, reproductive allocation was assumed to be constant and success was scaled to observed abundances of recruits. Stable-age distributions were calculated from the life and fertility tables, which also provided an estimate of the expectation of further life and the finite rate of population increase in the Wainui and Ohinepaka Bay populations. Stable age-distributions were compared to actual distributions determined by random transect using single classification χ^2.

2.2.3 Analysis

Survivorship of tagged plants was analysed using the survival analysis module within Prism 3.0 (Graphpad Software Inc., 1999). Growth rates were generally analysed as two-way ANCOVAs using site and time as independent variables. Initial size was used as covariate. Pearson product moment correlations were conducted on growth in relation to initial size. Where appropriate, data were transformed to meet the assumptions of normality and homogeneity of variance.

2.2.4 Definitions

Growth in *E. radiata* is fairly continuous; there are no discrete stages that allow easy categorisation. However, in this study a 'recruit' defines any individual <60mm in length. 'Juveniles' range in size up to 250mm. 'Immature' plants have reached canopy height and are beginning to develop secondary lamina, but do not yet have sori. 'Mature' individuals have well-developed secondary lamina and generally have sori.

2.3 Results

2.3.1 Spatial Patterns in Morphology, Biomass, and Density

Significant morphological differences in mature *E. radiata* were found amongst the three sites in this study. There was a consistent statistical difference (Table 3) between the Ohinepaka Bay site and the Tory Channel site. *E. radiata* at Ohinepaka Bay had long thick stipes with short laminae and the greatest total length. In contrast, *E. radiata* in Tory Channel had short, thin stipes with significantly longer laminae. Accordingly, destructive sampling showed Ohinepaka Bay plants had the greatest mean biomass, with most of the additional biomass attributed to stipe size. Plants at Wainui Bay and Tory Channel had a similar stipe, lamina and total mean biomass. These morphological differences indicate contrasting patterns in growth allocation.

Table 3. Patterns in morphology, density and biomass. Mean size ± 1SE of mature *E. radiata* at Ohinepaka and Wainui Bays derived from random transects and destructive sampling performed at approximately quarterly intervals from winter 1995 to spring 1998. Data from Tory Channel are from March 1996 and September 1998. Right hand column gives results of one-way anova (a, b, c indicates results of Tukey HSD test, sites with the same letter were not significantly different at p<.05).

	Ohinepaka Bay	Wainui Bay	Tory Channel	
		Random Transects		
Stipe-diameter (mm)	14.2 ± 0.15 **a**	13.2 ± 0.14 **b**	10.3 ± 0.41 **c**	$F_{(2,814)}$=60.0 p<0.0001
Stipe-length (mm)	306.8 ± 7.98 **a**	224.6 ± 6.08 **b**	188.0 ± 15.99 **b**	$F_{(2,814)}$=44.6 p<0.0001
Lamina-length (mm)	337.1 ± 6.74 **a**	337.9 ± 6.47 **a**	432.2 ± 22.35 **b**	$F_{(2,814)}$=17.3 P<0.0001
Total-length (mm)	643.9 ± 9.94 **a**	562.5 ± 9.71 **b**	620.3 ± 31.26 **ab**	$F_{(2,814)}$=15.8 P<0.0001
Stipe-volume (cm^3)	56.5 ± 2.07 **a**	36.03 ± 1.45 **b**	30.25 ± 3.25 **b**	$F_{(2,791)}$=39.5 P<0.0001
Stipe-length: lamina-length ratio	1.09 ± 0.04 **a**	0.75 ± 0.03 **b**	0.60 ± 0.08 **b**	$F_{(2,790)}$=31.3 P<0.0001
Density (plants.m^{-2}) mature	4.99 ± 0.32 **a**	3.85 ± 0.18 **b**	2.75 ± 0.48 **b**	$F_{(2,278)}$=8.8 P=0.0002
Density (plants.m^{-2}) immature	2.82 ± 0.35 **a**	2.40 ± 0.20 **a**	2.1 ± 0.22 **a**	$F_{(2,278)}$=0.2 P=0.84
Density (plants.m^{-2}) all	7.81 ± 0.49 **a**	6.25 ± 0.28 **b**	4.85 ± 0.45 **b**	$F_{(2,278)}$=6.9 P=0.0002
		Destructive sampling		
Stipe biomass (g_{wet})	58.08 ± 5.18 **a**	33.14 ± 3.08 **b**	24.18 ± 4.37 **b**	$F_{(2,190)}$=12.2 P<0.0001
Lamina biomass (g_{wet})	253.9 ± 19.09 **a**	199.69 ± 15.44 **ab**	173.24 ± 28.46 **b**	$F_{(2,197)}$=3.39 P=0.035
Total biomass (g_{wet})	307.87 ± 17.54 **a**	232.49 ± 17.54 **ab**	197.4 ± 21.6 **b**	$F_{(2,197)}$=5.11 P=0.007

Mature *Ecklonia* at Ohinepaka Bay were significantly more dense than at Tory Channel, although there was no significant difference in mature *Ecklonia* density between Wainui Bay

and Tory Channel (Table 3). The abundance of immature plants did not show any significant patterns, possibly reflecting the high variability of immature plants within sites.

Estimates of total standing-stock ($g_{wet}.m^{-2}$) and productivity ($g_{dry}.m^{-2}.yr^{-1}$) were greater in Ohinepaka Bay than Wainui Bay (Table 4). However, immature plants did not show a significant difference between sites. Details of the analysis were: ANOVA of the standing stock of mature plants gave $F_{(1,144)}=10.4$; $p=.0015$. ANOVA of the standing stock of immature plants gave $F_{(1,144)}=3.68$; $p=.057$. ANOVA of total standing stock gave $F_{(1,144)}=11.7$; $p=.0008$. Although similar comparisons were not able to be made with Tory Channel, the standing stock of mature plants was considerably lower than Akaroa Harbour sites.

Table 4. Mean standing stock, and productivity estimates ± 1SE of *E. radiata* at Ohinepaka and Wainui Bays derived from random transects and destructive sampling performed at approximately quarterly intervals from winter 1995 to spring 1998. Data from Tory Channel are from March 1996 and September 1998.

Measured parameter	Ohinepaka Bay n=109	Wainui Bay n=152	Tory Channel n=47
Standing stock ($g.m^{-2}$) mature	1764.2 ± 161.4	1195.2 ± 91.6	324.7 ± 72.1
Standing stock ($g.m^{-2}$) immature	72.7 ± 14.4	38.3 ± 6.0	-
Standing stock ($g.m^{-2}$) total	1836.9 ± 61.5	1233.5 ± 91.9	-
Productivity ($g_{dry}.m^{-2}.yr^{-1}$)	471.8 ± 59.9	233.2 ± 21.9	-

2.3.2 Temporal Patterns in Morphology, Biomass, and Density

Temporal variation in the morphology of randomly sampled plants was investigated at the two Akaroa sites using two way ANOVA. The sites differed significantly in stipe length ($F_{(1,648)}=35.9$; $p<0.0001$) but had similar lamina lengths ($F_{(1,648)}=0.014$; $p=0.907$). There was no difference in stipe length between sampling times ($F_{(5,648)}=0.7$; $p=0.647$) (Figure 5a), however significant temporal patterns were seen in lamina length ($F_{(5,648)}=15.45$; $p=0.005$) (Figure 5b). Lamina length fluctuated seasonally: fronds were generally longest over summer and shortest during winter, probably as a result of lamina erosion outpacing lamina growth. Both morphological parameters exhibited a significant interaction between site and time; Stipe length $F_{(5,648)}=5.45$, $p<0.001$, Lamina length $F_{(5,648)}=7.8$, $p<0.001$. This lack of additivity suggests that different processes and responses are occurring at the sites at the same time.

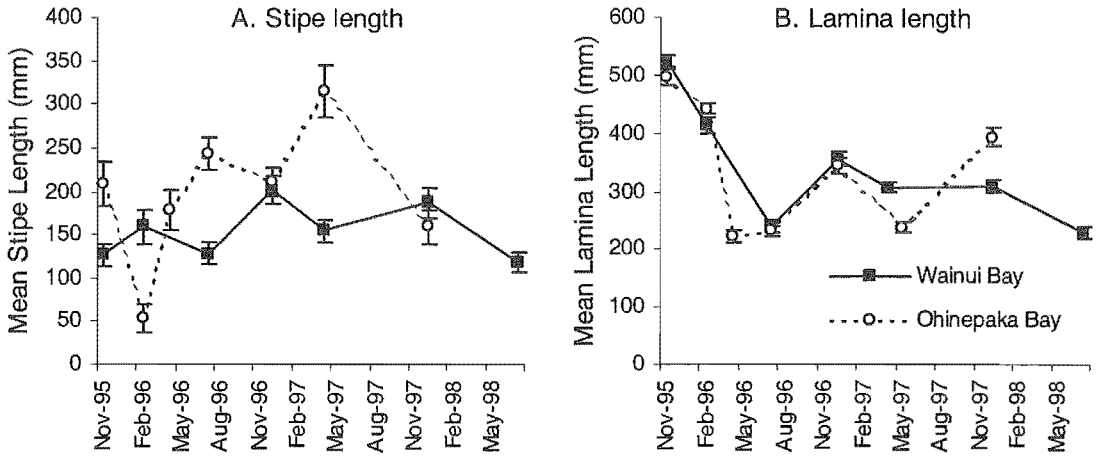

Figure 5 A-B. Mean stipe length and lamina length of randomly sampled *E. radiata* through time at Ohinepaka and Wainui Bays. ± 1 SE. Times were approximately quarterly between spring 1995 and summer 1998.

The mean density of mature *E. radiata* (Figure 6a) was higher at Ohinepaka Bay ($F_{(1,212)}$=15.3, p<0.0001) and although overall abundance did not vary with time ($F_{(6,212)}$=2.1, p=0.54), there was a greater degree of variability at the Ohinepaka Bay site. The numbers of immature *E. radiata* (Figure 6b) however, fluctuated significantly with time ($F_{(6,212)}$=2.94, p=0.009), peaking in April 1996 at Ohinepaka Bay and in July 1996 at Wainui Bay. There was no statistical difference in immature plant abundance between sites ($F_{(1,212)}$=0.341, p=0.56), but, the interaction between site and time was significant ($F_{(6,212)}$=2.24, p=0.041).

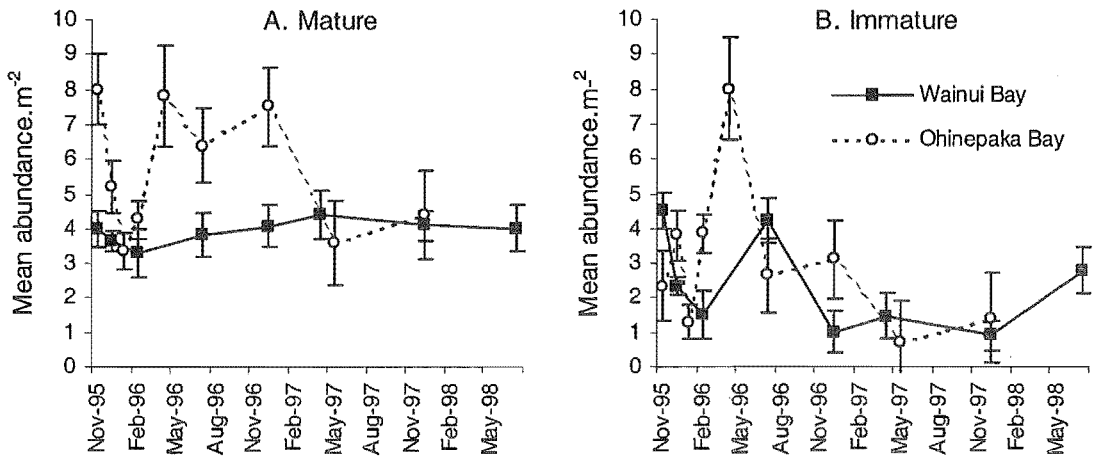

Figure 6 A-B. Mean abundance ± 1 SE of randomly sampled *E. radiata* through time at Ohinepaka and Wainui Bays. Mature plants are those with sori (stipe volume > ~10cm^3) and that form a canopy, immature plants do not possess sori and do not form a canopy (includes recruits and juveniles).

The standing-stock of mature *E. radiata* (Figure 7a) showed significant differences between sites ($F_{(1,134)}$=12.9, p<0.0001) and through time ($F_{(5,143)}$=2.64, p=0.026), being initially greater at Ohinepaka Bay. The standing-stock at Ohinepaka Bay decreased with time, while remaining reasonably constant in Wainui Bay (Figure 7a), however, the interaction term was not significant ($F_{(5,134)}$=1.6, p=0.173). There were no significant patterns in the standing stock of immature *E. radiata* between sites or across sampling times (Figure 7b).

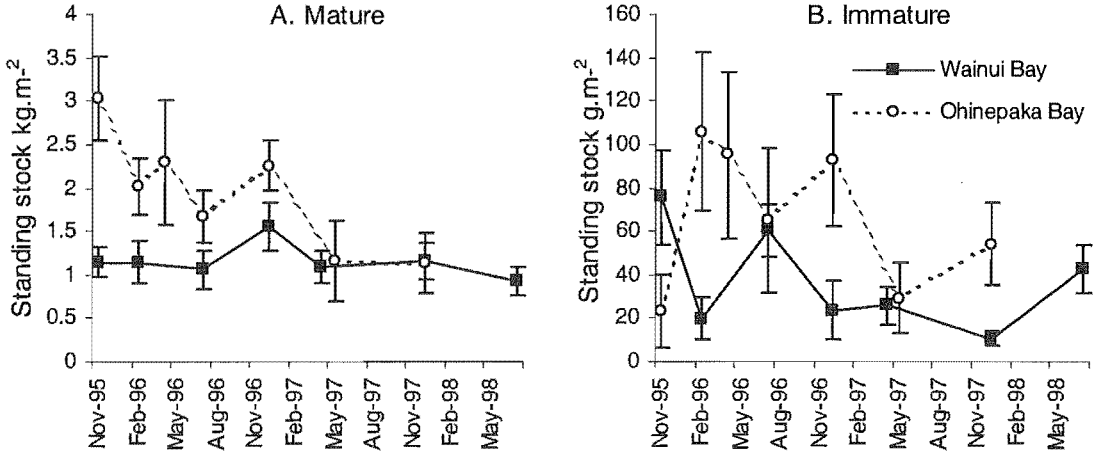

Figure 7 A-B. Mean standing stock of randomly sampled *E. radiata* through time at Ohinepaka and Wainui Bays. Standing stock was estimated as a function of stipe diameter and lamina length. Mature plants are those with sori (stipe volume > ~10cm^3). Wet-weight was estimated as a function of stipe diameter and lamina length ± 1 SE.

2.3.3 Growth

Stipe and lamina elongation were used to assess differences in growth between sites. Three-way ANCOVA, using initial size as a covariate, found significant differences in growth rate between sites for elongation rate of both stipe (Table 5) and lamina (Table 6). There were no significant variation in growth with time, although stipe growth rate and net lamina growth rate generally displayed the same temporal trends of higher growth during late-spring/early summer (November/December) and low growth during autumn/early winter (May/June) (Figure 8 & Figure 9). Most importantly, there were significant third-order interactions between time, site, and initial size in both stipe and lamina elongation which may be attributed to a large peak in stipe elongation at Ohinepaka Bay during spring/summer 1996 and a large trough in net lamina elongation (>350mm) at Wainui Bay during summer/autumn (March/April) 1996. Additionally these interactions may also suggest size-specific schedules of growth, possibly reflecting suppression of smaller individuals by larger individuals. Gross lamina elongation (from hole-punching) showed significant temporal

patterns (Table 7) that were similar to, but less variable than, net lamina elongation (Figure 9). Importantly however, there was no statistical difference in the gross lamina elongation between sites. This suggests a higher rate of lamina erosion occurring at Wainui Bay than at Ohinepaka Bay. Additionally, stipe growth rates were generally low (Figure 8), and this may explain the absence of visible stipe growth rings in these populations (De Wreede, 1984).

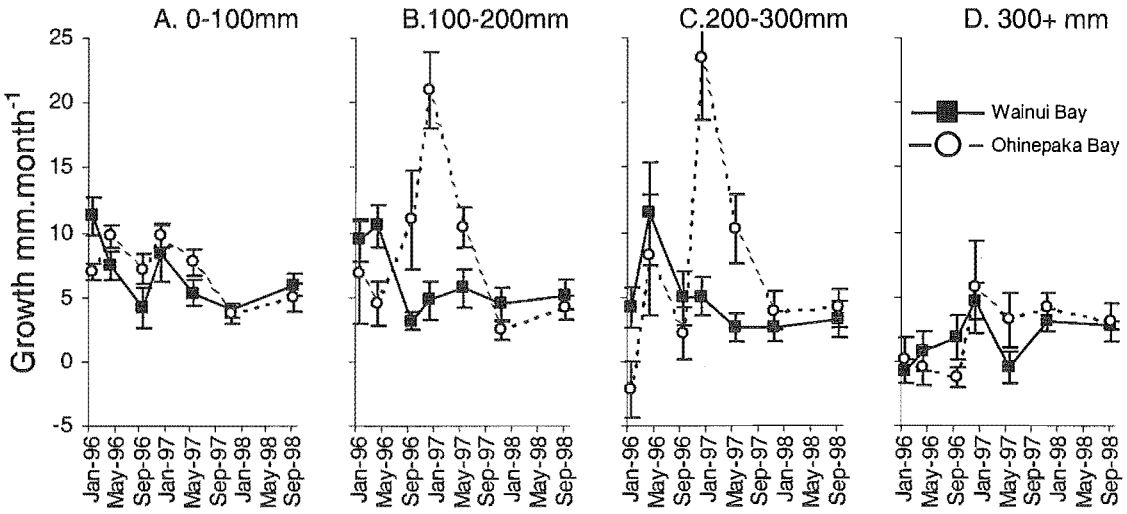

Figure 8 a-d. Mean stipe length growth rate of tagged *E. radiata* in Wainui and Ohinepaka Bays grouped by initial size category ± 1 SE.

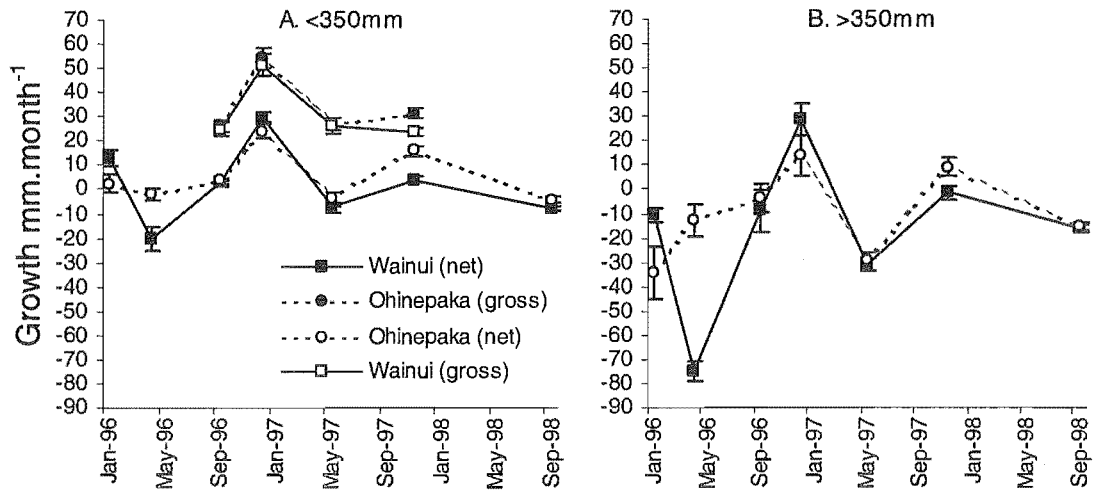

Figure 9 a-b. Mean net and gross lamina length growth rate of tagged *E. radiata* in Wainui and Ohinepaka Bays grouped by initial size category ± 1 SE.

Table 5. Stipe elongation rate

Effect	df	MS	F	p-level
Time	6	0.7834	1.278	0.387
Site	1	0.4107	6.634	0.010*
Size	3	0.3149	4.762	0.116
Time x Site	6	0.6129	9.900	0.000**
Time x Size	18	0.1599	0.748	0.728
Site x Size	3	0.0661	1.068	0.362
Time x Site x Size	18	0.2044	3.302	0.000**
Error	1066	0.0619		

Table 6. Lamina elongation rate (net)

Effect	df	MS	F	p-level
Time	6	38.020	3.207	0.091
Site	1	3.4374	6.948	0.009**
Size	1	1.7478	1.327	0.455
Time x Site	6	11.857	23.97	0.000**
Time x Size	6	4.8613	1.508	0.315
Site x Size	1	1.3175	2.663	0.103
Time x Site x Size	6	3.2230	6.515	0.000**
Error	1093	0.4947		

Table 7. Lamina elongation rate (gross)

Effect	df	MS	F	p-level
Time	3	6.9490	101.5	0.002**
Site	1	0.3936	1.733	0.190
Time x Site	3	0.0685	0.302	0.824
Error	126	0.2271		

Table 5 - Table 6. Results of three-way ANCOVA performed on the growth rates of tagged *E. radiata*. Time = 7 growth periods between spring 1995 and spring 1998; Site =Wainui Bay and Ohinepaka Bay (random factor); Size = Initial size class: Stipe length = <100mm, 100-200mm, 200-300mm, >300mm; Lamina length = <350mm, >350mm. Initial sizes were used as covariate. ** is significant at p<.01, * is significant at p<.05.

Table 7. Result of two-way ANOVA of gross lamina growth rate of tagged *E. radiata*, estimated b hole-punching. Time = 4 growth periods between autumn 1996 and spring 1997; Site = Wainui Bay and Ohinepaka Bay (random factor). ** is significant at p<.01.

2.3.4 Survival

The relative impacts of age and size on survival rate were examined in Wainui and Ohinepaka Bays. Survival among tagged plants was examined in relation to estimated biomass (size) and estimated age (derived from stipe-volume). Within the tagged plants of Wainui Bay survival varied significantly with respect to initial biomass but not with age, (Table 8). Larger (>320g) plants had lower rates of survival than smaller plants (Figure 10 a-b).

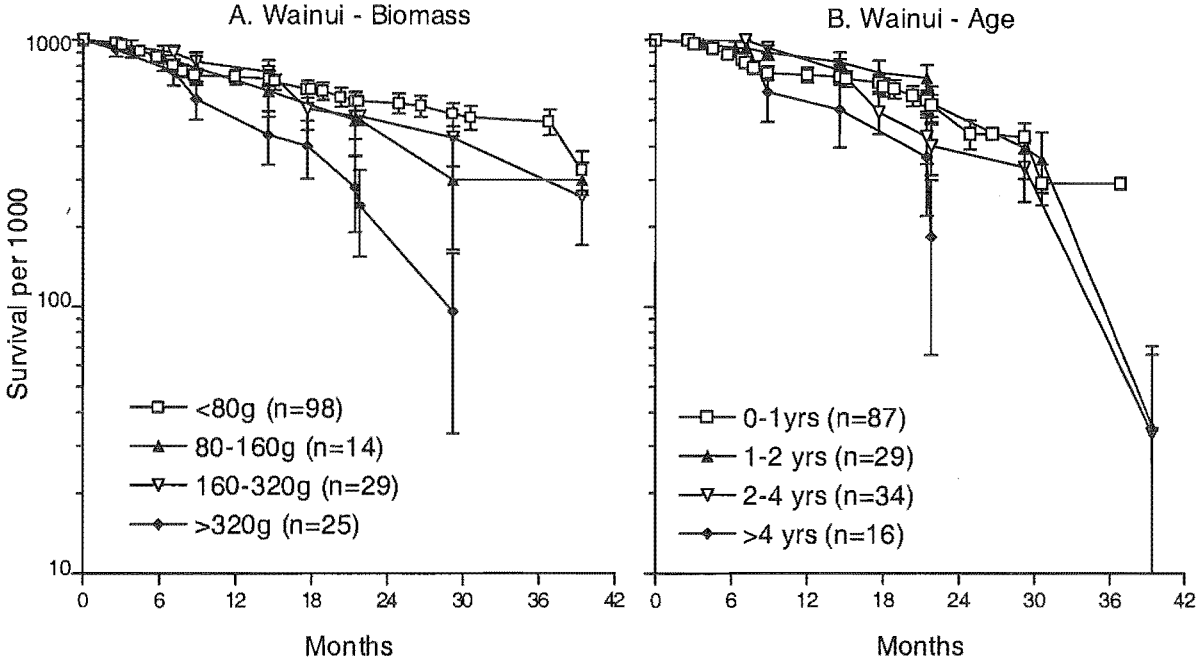

Figure 10 A-B Survival curves of *E. radiata* in Wainui Bay grouped by initial biomass (a) and initial age (b). Survival was expressed in terms of the number of months tagged *E. radiata* survived, and includes censored data of individuals that survived throughout the experiment. ± 1 SE.

Survival at the Ohinepaka Bay site was significantly related to initial age (Table 8, Figure 11b). Plants initially aged between 1 and 2 years had significantly higher survival than other age categories. Survival at Ohinepaka Bay was generally unrelated to biomass across size-categories (Table 8, Figure 11a). However, within a cohort of 47 juvenile *E. radiata* less than 200mm in total-length, survival was significantly related to initial size (χ^2=10.0, df=2, p<.01); median survival time of larger members of the cohort (150-200mm) was 26 months, while the smaller members (<100mm) of the cohort had a median survival time of only 5.5 months. The intermediate sized members of the cohort (100-150mm) came in between with a median survival time of 14.8 months.

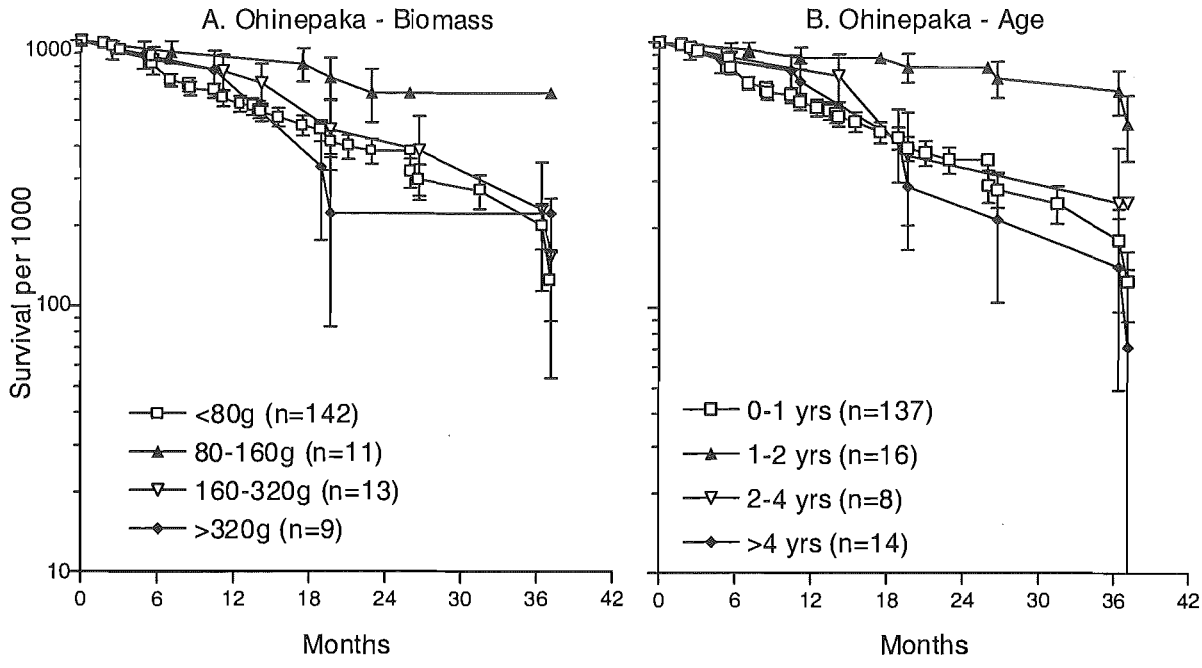

Figure 11 A-B. Survival curves of *E. radiata* in Ohinepaka Bay grouped by initial biomass (a) and initial age (b). Survival was expressed in terms of the number of months tagged *E. radiata* survived, and includes censored data of individuals that survived throughout the experiment. ± 1 SE.

Table 8. Results of survival analysis by logrank test. Mortality with respect to initial age (derived from stipe volume) and biomass (size) were examined at two sites. Plants were divided into four categories based on initial age and initial biomass. Median survival time represents time in months for 50% of plants to die.

Median Survival Time (months)	Age Category (years)				χ^2	df	p
	0-1	1-2	2-4	>4			
-Wainui Bay	24.9	29.2	21.4	21.4	5.63	3	0.131
-Ohinepaka Bay	17.5	37.1	19.6	18.9	11.44	3	0.009**

Median Survival Time (months)	Biomass Category (g)				χ^2	df	p
	<80	80-160	160-320	>320			
-Wainui Bay	36.9	21.4	29.2	14.6	13.20	3	0.004**
-Ohinepaka Bay	17.5	19.6	>36	18.9	6.538	3	0.088

In contrast to the high survival among the smallest tagged plants (min. size ~ 75mm total length) survival among mapped recruits (min. size ~ 4mm total length) was generally poor. Of the 26 new recruits initially mapped in Wainui Bay, only one plant was found intact on a subsequent visit 2 months later. In Ohinepaka Bay, 44 of the 61 recruits mapped were present 2 months later. Eight months later, 32 plants remained (mean length 152.0mm ± 22.5mm SE). The survival probabilities of these mapped recruits were not included in the

determination of transition matrices or life tables because of their extreme variability, and also because of the difficulty in extrapolating survivorship over a one year period. In Tory Channel, by September 1998 only 8 of the original 60 tagged plants remained, indicating a survival rate of ~45% per year.

2.3.5 Reproduction and Recruitment

The numbers of spores released per cm^2 of sori were higher in sori classified as full compared to those classified as spent ($F_{(1,9)}$=18.67; p=0.0025) (Figure 12a). On average, full sori released 1.2 x 10^5 spores.cm^{-2}; spent sori released 3.5 x 10^4 spores.cm^{-2}. The relationship between spores released and (full) sori area is well described by a linear model (R^2= 0.92) (Figure 12b). Similarly, spores released per sorus area did not vary significantly over a range of sori areas ($F_{(4,20)}$=2.01; p=0.12).

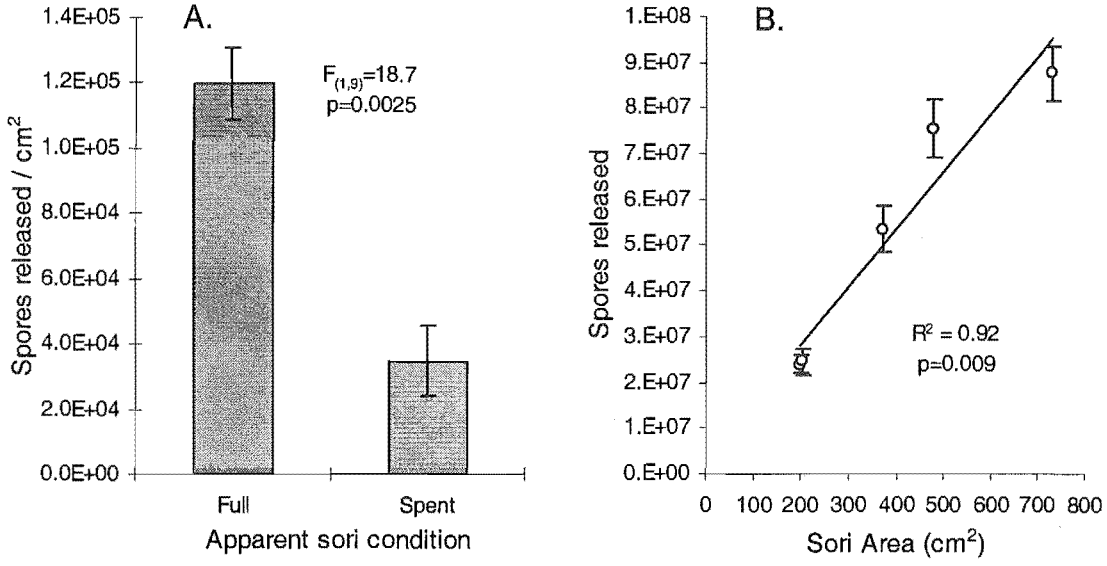

Figure 12 A-B. (a) The mean number of spores released from full and spent sori ± 1 SE. Full and spent sori were subjectively assessed on whether sori were lighter (spent) or darker (full) than surrounding tissue. (b) The relationship between the number of spores released from full *E. radiata* sori and sori area (max. width x max. length). Spore release was induced by partially drying sori and then placing in 250ml of filtered sea water. ± 1 SE.

There was a positive relationship between biomass and total sori area in destructively sampled plants from Wainui and Ohinepaka Bays (Table 9). However, the relationship between age (stipe-volume) and total sorus area was poor at both Ohinepaka (r=0.10) and Wainui Bays (r=0.39) suggesting that reproductive output is not particularly related to age. The minimum age and size at which sori are formed was assessed by logit regression, which describes the relationship between a continuous independent variable (age or biomass) and a binary dependent variable (presence or absence of sori). By this method, *Ecklonia* in Wainui Bay develop sori at ~122g or ~1.6 years and *Ecklonia* in Ohinepaka Bay develop sori at

~160g or ~1.7 years (Table 10). These results support the assumptions (refer 2.2.2.4) made in the assessment of reproductive output subsequently used in the construction of transition matrices and life and fertility tables.

Table 9. Relationship between sori area and biomass and between sori area and age (derived from stipe-volume) in destructively sampled *E. radiata* from Wainui and Ohinepaka Bays.

		Wainui Bay			Ohinepaka Bay		
		r	p	n	r	p	n
Total sori area (cm^2)	v biomass (wet)	0.55	0.000	38	0.58	0.002	26
	v age (stipe volume)	0.39	0.017	38	0.10	0.724	26

Table 10. The minimum size (biomass) and age at which sori are produced in *E. radiata*. Values were determined by logit regression of biomass/ age (stipe-volume) against presence or absence of sori. Age was determined from stipe-volume using relationship in Table 2.

	Wainui Bay				Ohinepaka Bay			
	Minimum	X^2	p	n	Minimum	X^2	p	N
Biomass	121.9g	86.32	0.000	98	161.2g	48.22	0.000	85
Age	1.57 yrs	55.97	0.000	100	1.68 yrs	24.53	0.000	86

The ratio between spent and full sori area on mature *E. radiata* was used to determine the time at which spores are released naturally. The ratio of full to spent sori peaks in late autumn/early winter (Apr-May), and declines markedly by spring / summer (Nov-Dec), suggesting that the majority of spores are released during winter (Figure 13).

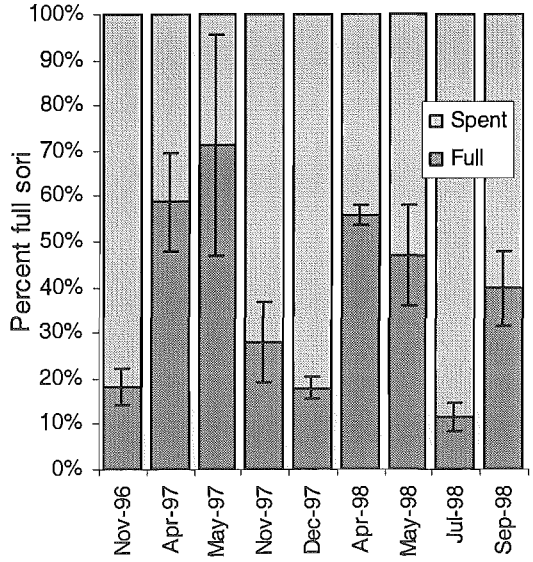

Figure 13. Seasonal variation in the proportional area of full and spent sori measured on destructively sampled *E. radiata*. ± SE. Full and spent sori were subjectively assessed on whether sori were lighter (spent) or darker (full) than surrounding tissue

Spatial patterns of recruitment were extremely variable at both the Wainui and Ohinepaka Bay sites. No *E. radiata* recruits were ever observed on any of the concrete settling slabs placed in Wainui and Ohinepaka Bay. Observations indicated that plants on natural substrata often recruited in clumps. As a result, overall densities of recruits were low (generally $<0.5.m^{-2}$) (Figure 14a), even though large numbers of new recruits were sometimes found in very close proximity.

New recruits are first visible in mid-spring (October-November). In October 1997 the average length of new recruits found on dead holdfasts in Wainui Bay was 9.64mm ± 1.18mm SE. By April 1998 the mean length of recruits found was 43.66mm ± 9.10mm SE (Figure 14b). In Ohinepaka Bay new recruits with a mean size of 27.0mm ± 2.6mm SE were found in March 1998; these plants were followed until November 1998 at which time their mean length was 161.3mm ± 23.0mm SE.

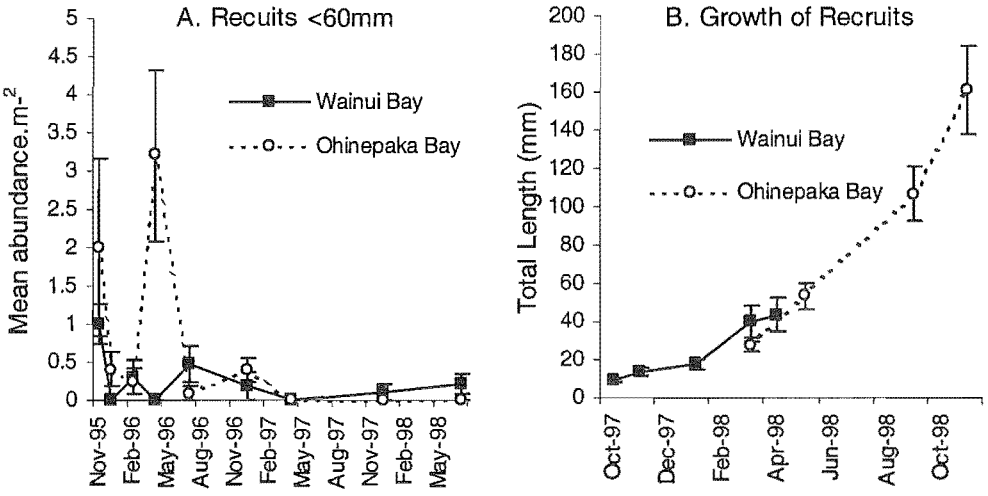

Figure 14 A-B. (a) Mean abundance of newly recruited laminarians <60mm in length through time at Ohinepaka and Wainui Bays. ± 1 SE. (b)Composite growth curve of newly recruited *E. radiata* constructed from the mean total length of recruits observed on dead holdfasts (Wainui), and the mean total length of a cohort of new recruits followed through time (Ohinepaka). ± 1 SE.

2.3.6 Stable Size-Distributions

The stable biomass-distributions of *E. radiata* at Wainui and Ohinepaka Bays were determined by projection of their respective transition matrices through 30 iterations (Table 12, Table 13). In these matrices, q_x is the proportion of mortality within each biomass category, w is the stable biomass distribution projected by the matrix, λ is the finite rate of increase of the population, and λ_r is the finite rate of increase with no contribution from recruitment. The values of λ found for Wainui and Ohinepaka Bays were estimated at 0.93 and 0.86 respectively. Given the observed rates of size-specific survival and estimated

fecundity in this study, *E. radiata* populations appear to be declining in these localities in Akaroa Harbour.

An important general pattern in both the predicted and observed biomass-distributions was a bimodal shape across size class. Wainui and Ohinepaka Bays both showed a peak in the <20g category and another peak in the 160-320g category (Figure 15h, Figure 16h). At Wainui Bay there was considerable variation in the observed data through season, with all periods being significantly different from the predicted distribution (Table 11). However, analysis of the average biomass distribution resulted in a borderline significant difference (χ^2 =14.2, p=0.0474). This suggests that the observed size distribution of *E. radiata* in Wainui Bay may approach, on average, the stable size-distribution predicted by transition matrices. At Ohinepaka Bay the biomass distribution observed in autumn 1996 was not significantly different from the predicted stable size distribution. However, on average, the predicted and observed distributions were different, with cell χ^2 indicating the difference lay in the 320-640g size class.

Despite the bimodal size distribution, the transition probabilities derived in this study suggest that small plants are not suppressed beneath larger plants. In Wainui Bay 59% of all <20g individuals grew into a larger size category in one year, and 96% of 20-40g individuals made the transition to larger categories. Data for Ohinepaka Bay are 47% and 46% respectively. <20g plants that do not progress to larger categories generally die; no plants remained within this size category in Wainui Bay, and only 2% remained in Ohinepaka Bay. Beyond 160g, 30-40% of plants remain within each size category from year to year.

Table 11. Comparison of observed biomass distributions *E. radiata* with the stable distribution predicted using transition matrices.

	Predicted v Observed		
Wainui Bay	χ^2	**df**	**p**
Spring 1995	28.98	7	0.000**
Summer 1996	35.69	7	0.000**
Winter 1996	30.16	7	0.000**
Summer 1997	50.21	7	0.000**
Winter 1997	25.63	7	0.001**
Summer 1998	29.98	7	0.000**
Winter 1998	43.53	7	0.000**
Average	**14.22**	**7**	**0.047***
Ohinepaka Bay	χ^2	**df**	**p**
Spring 1995	60.46	7	0.000**
Summer 1996	55.01	7	0.000**
Autumn 1996	11.02	7	0.138
Winter 1996	16.73	7	0.019*
Summer 1997	32.71	7	0.000**
Winter 1997	94.09	7	0.000**
Summer 1998	24.46	7	0.001**
Average	**17.57**	**7**	**0.014***

Table 12. Biomass transition matrix for Wainui Bay

Size class in year 2	Size class in year 1(g)							
	0-20	21-40	41-80	81-160	161-320	321-640	641-1280	1280+
0-20g	0	0	0	0	0.59	0.98	0.25	0.02
21-40g	0.07	0	0	0	0	0	0	0
41-80g	0.15	0.19	0.03	0.02	0	0	0	0
81-160g	0.33	0.42	0.17	0.14	0.02	0	0	0
161-320g	0.04	0.19	0.56	0.26	0.39	0.14	0	0
321-640g	0	0.12	0.06	0.07	0.34	0.31	0.14	0
641-1280g	0	0.04	0	0	0.04	0.11	0.29	0
1280+g	0	0	0	0	0	0	0.07	0
q_x	0.41	0.04	0.19	0.51	0.21	0.45	0.50	1.00
w	0.32	0.03	0.06	0.17	0.22	0.16	0.04	0.00
λ	0.93							
λ_r	0.61							

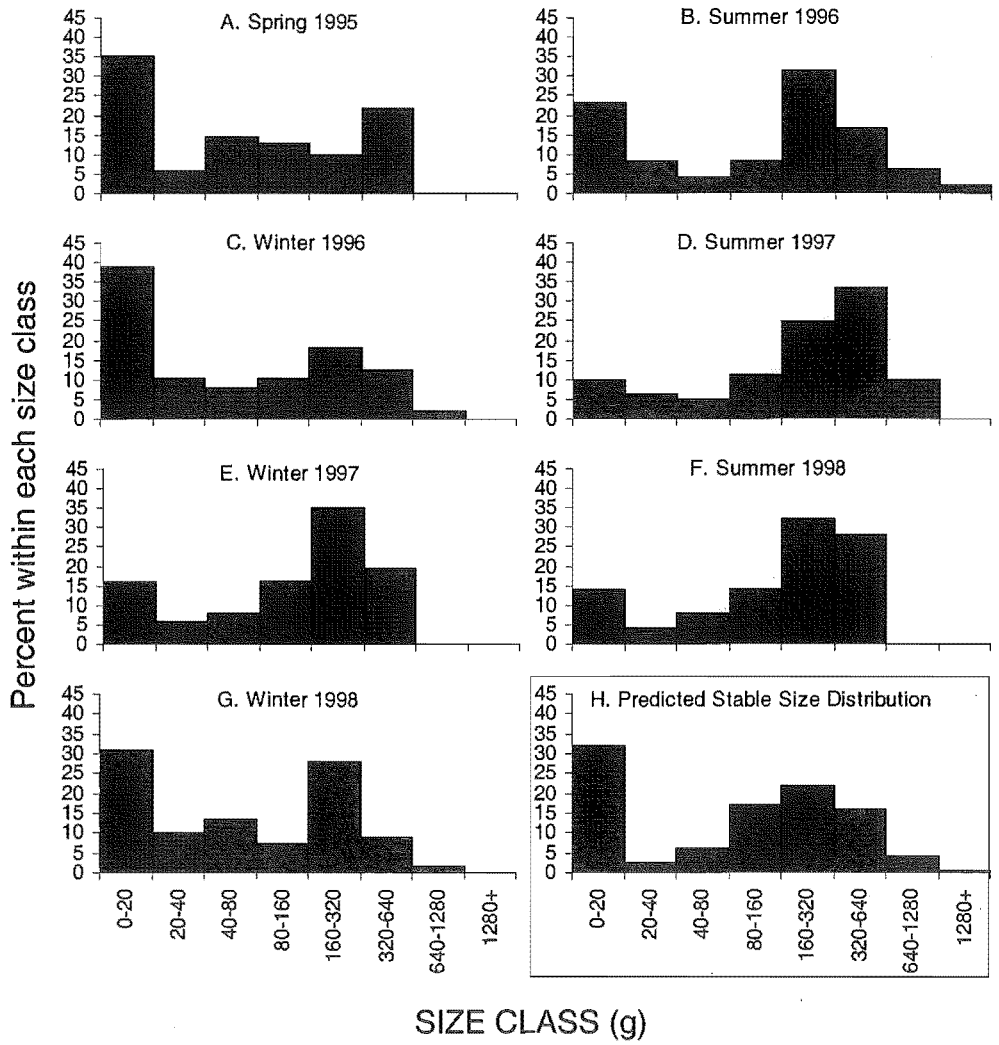

Figure 15 A-H. (a-g) Observed biomass-distribution of *E. radiata* in Wainui Bay through time. Biomass was estimated as a function of stipe diameter and lamina length. (h) Predicted stable biomass-distribution of *E. radiata*. The distribution is derived from transition probabilities observed in tagged plants.

Table 13. Biomass transition matrix for Ohinepaka Bay

Size class in year 2	Size class in year 1(g)							
	0-20	21-40	41-80	81-160	161-320	321-640	641-1280	1280+
0-20g	0.02	0.04	0	0	0.42	0.86	0.34	0.013
21-40g	0.10	0.02	0.02	0	0	0	0	0
41-80g	0.17	0.18	0.07	0.17	0	0	0	0
81-160g	0.15	0.12	0.24	0.29	0.03	0	0	0
161-320g	0.05	0.14	0.34	0.17	0.45	0.19	0.40	0
321-640g	0	0.02	0	0.05	0.18	0.38	0	0
641-1280g	0	0	0	0	0.05	0	0	0
1280+g	0	0	0	0	0	0	0	0
q_x	0.51	0.48	0.32	0.32	0.29	0.44	0.60	1.00
w	0.31	0.04	0.08	0.11	0.29	0.15	0.02	0.00
λ	0.86							
λ_r	0.64							

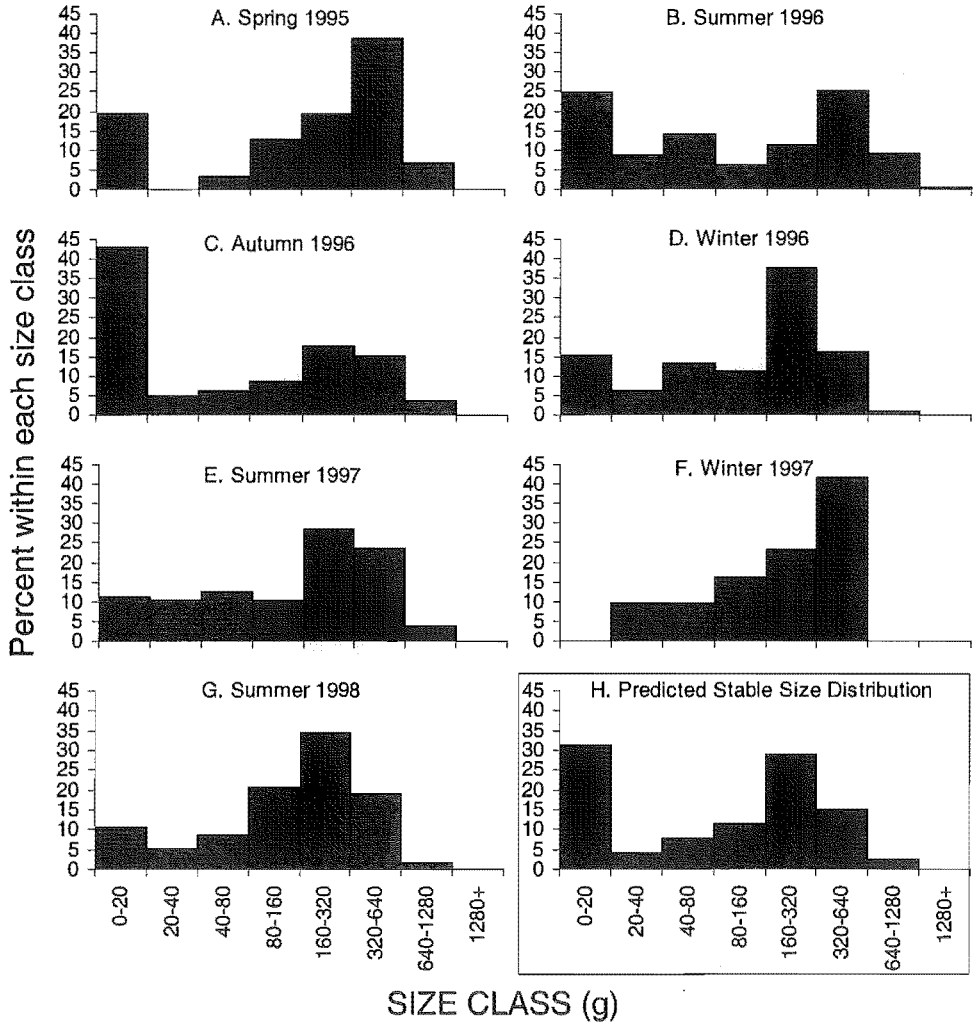

Figure 16 A-H. (a-g) Observed biomass-distribution of *E. radiata* in Ohinepaka Bay through time. Biomass was estimated as a function of stipe diameter and lamina length. (h) Predicted stable biomass-distribution of *E. radiata*. The distribution is derived from transition probabilities observed in tagged plants.

2.3.7 *Stable Age-Distributions*

Life and fertility tables were used to estimate the stable age-distribution at Wainui (Table 15) and Ohinepaka Bays (Table 16). Life tables predict an age-structure in *E. radiata* at Wainui and Ohinepaka Bays that decreases smoothly from a large number of young individuals to smaller numbers of older individuals (Figure 17h, Figure 18h). Predicted age structure was compared to actual age distributions using single classification χ^2. In Wainui Bay, the predicted stable age-distribution was not significantly different from observed distributions during summer 1996, winter 1997, and winter 1998 (Figure 17a-g), and the mean age distribution across time was also not significantly different from predicted (Table 14). In Ohinepaka Bay, the predicted stable age-distribution only agreed with observation during summer 1997 (Table 14), but was not significantly different on average (Figure 18a-g). Large peaks in observed first-year categories at both sites reflect the appearance of new recruits.

The finite rates of population increase (λ) estimated from life and fertility tables indicate that the population was increasing at Wainui Bay (λ=1.12), but remained steady at Ohinepaka Bay (λ=1.01). The expectation of further life (e_x) never exceeded three years (in macroscopic stages), and generally declined throughout life, this suggests that mortality was a function of age.

Table 14. Comparison of observed age distributions of *E. radiata* with the stable distribution predicted by life and fertility tables.

	Predicted v Observed		
Wainui Bay	χ^2	**df**	**p**
Spring 1995	18.43	6	0.005**
Summer 1996	1.955	6	0.924
Winter 1996	20.78	6	0.002**
Summer 1997	29.60	6	0.000**
Winter 1997	12.42	6	0.053
Summer 1998	52.93	6	0.000**
Winter 1998	8.039	6	0.235
Average	**4.009**	**6**	**0.675**
Ohinepaka Bay	χ^2	**df**	**p**
Spring 1995	26.38	6	0.000**
Summer 1996	39.94	6	0.000**
Autumn 1996	74.08	6	0.000**
Winter 1996	41.67	6	0.000**
Summer 1997	7.067	6	0.315
Winter 1997	66.72	6	0.000**
Summer 1998	23.39	6	0.001**
Average	**11.54**	**6**	**0.073**

Table 15. Life and fertility table for Wainui Bay. Abbreviations: q_x=proportionate mortality; l_x=proportion living at start of interval; d_x=proportion dying during interval; e_x=mean life expectancy; b_x=number of offspring per sporophyte age x; V_x=reproductive value of interval x.

Age (years)	q_x	l_x	d_x	e_x	b_x	V_x
0-1	0.227	1.000	0.227	2.976	0.000	0.000
1-2	0.256	0.773	0.198	2.704	0.359	0.278
2-3	0.247	0.575	0.142	2.461	0.719	0.413
3-4	0.270	0.433	0.117	2.103	0.719	0.312
4-5	0.423	0.316	0.134	1.696	0.719	0.227
5-6	0.400	0.183	0.073	1.571	0.719	0.131
6+	1.000	0.110	0.110	1.286	0.719	0.079
	Net replacement rate per generation (R_o)		1.440			
	Mean cohort generation time (T_c)		3.331			
	Finite rate of increase (λ)		**1.116**			

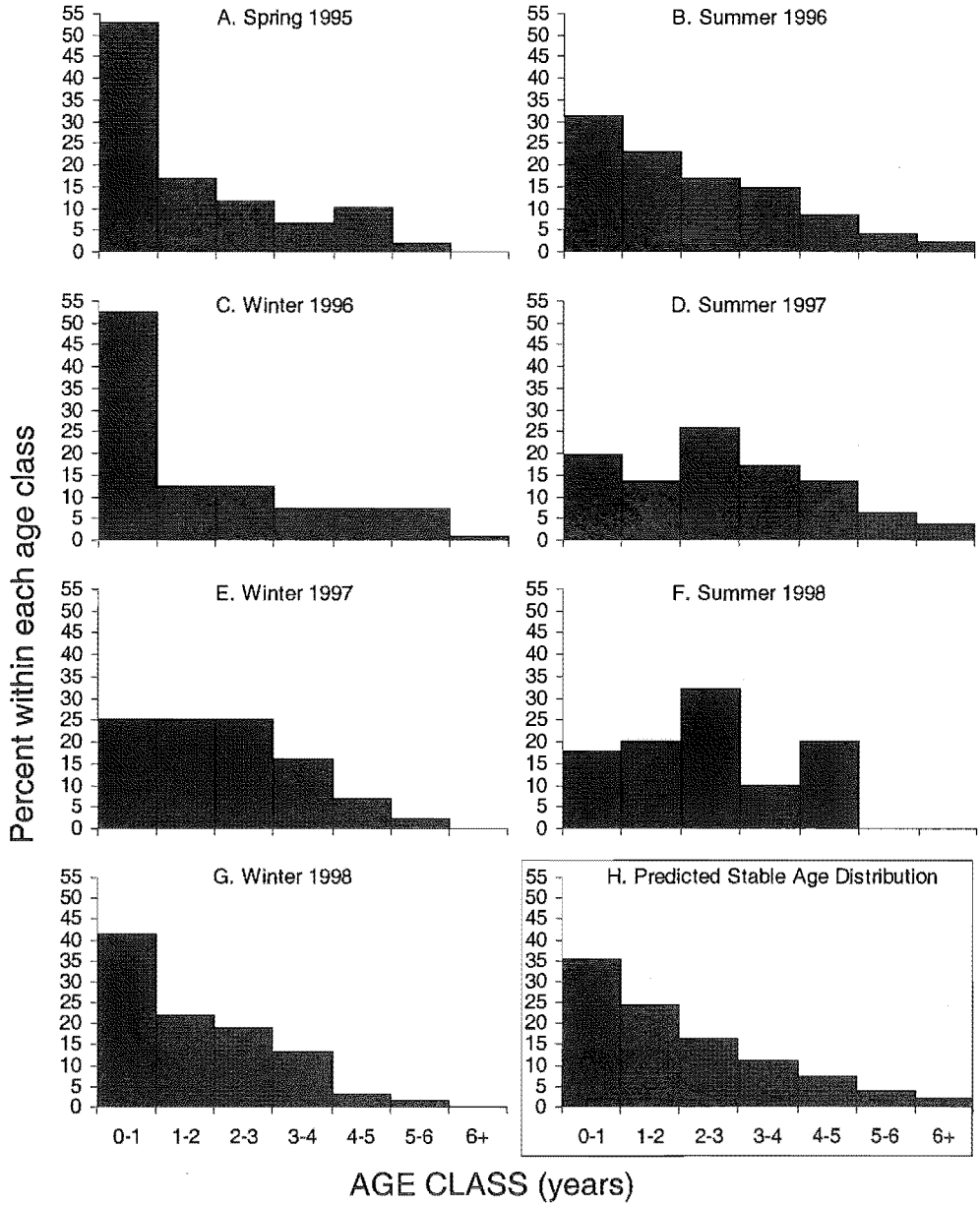

Figure 17 A-H. (a-g) Observed age distribution of *E. radiata* in Wainui Bay through time. Age was estimated from stipe volume. (h) Predicted stable age distribution of *E. radiata* in Wainui Bay. The distribution is derived from life and fertility tables constructed from tagged plant data.

Table 16. Life and fertility table for Ohinepaka Bay. Abbreviations: q_x=proportionate mortality; l_x=proportion living at start of interval; d_x=proportion dying during interval; e_x=mean life expectancy; b_x=number of offspring per sporophyte age x; V_x=reproductive value of interval x.

Age (years)	q_x	l_x	d_x	e_x	b_x	V_x
0-1	0.354	1.000	0.354	2.631	0.000	0.000
1-2	0.281	0.646	0.182	2.797	0.303	0.196
2-3	0.247	0.465	0.115	2.695	0.607	0.282
3-4	0.207	0.350	0.072	2.414	0.607	0.212
4-5	0.300	0.278	0.083	1.913	0.607	0.168
5-6	0.444	0.194	0.086	1.519	0.607	0.118
6+	1.000	0.108	0.108	1.333	0.607	0.065
	Net replacement rate per generation (R_o)		1.042			
	Mean cohort generation time (T_c)		3.430			
	Finite rate of increase (λ)		**1.012**			

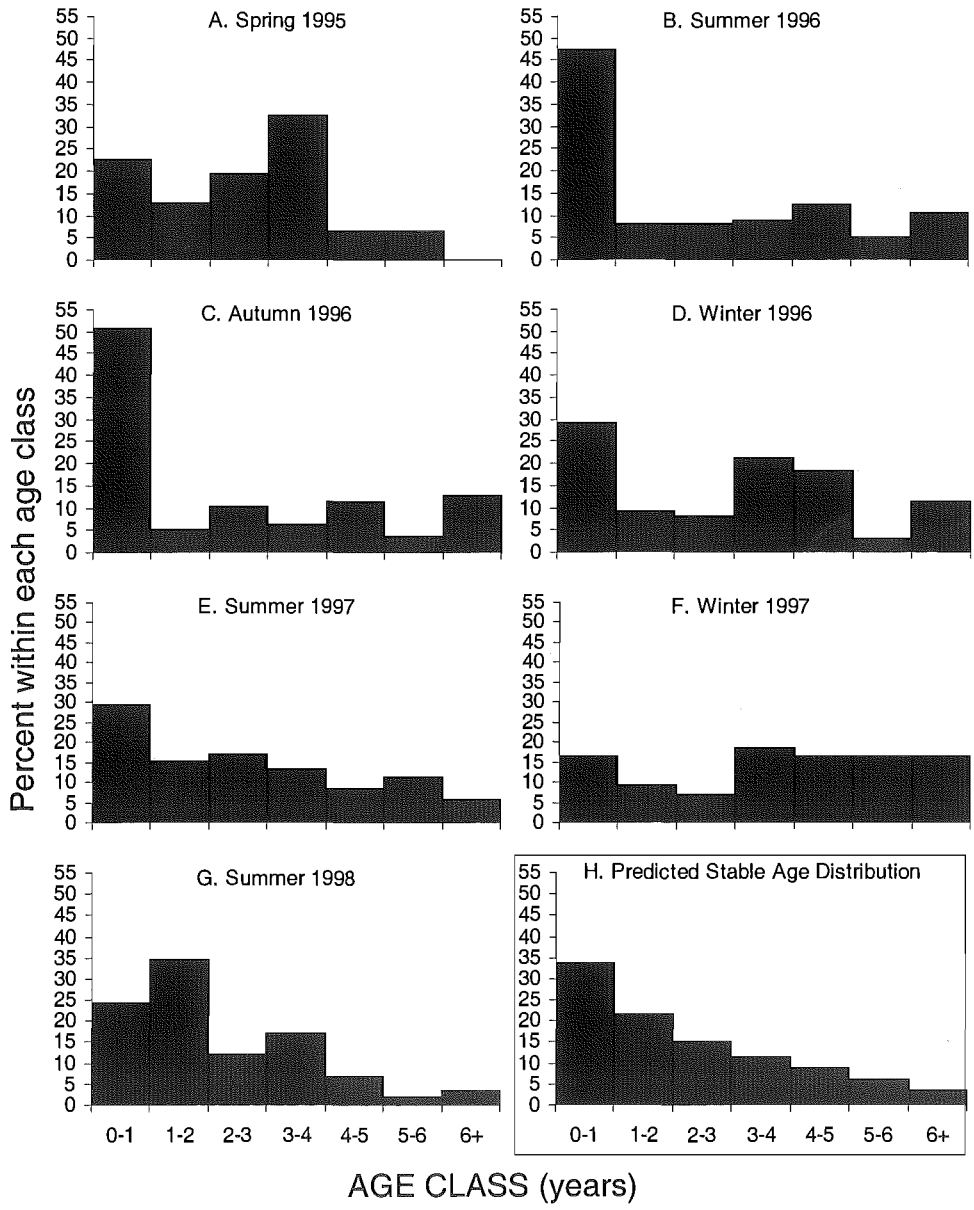

Figure 18 (a-g) Observed age distribution of *E. radiata* in Ohinepaka Bay through time. Age was estimated from stipe volume.(h) Predicted stable age distribution of *E. radiata* in Wainui Bay. The distribution is derived from life and fertility tables constructed from tagged plant data.

2.4 Discussion

This study found significant variation in the morphology of *Ecklonia* at both small and large scales within Akaroa Harbour, and between Akaroa Harbour and Tory Channel (Table 3). This variation in morphology may be related to the physiological constraints imposed by depth/light and exposure (Mann, 1971; Chapman, 1973; Gerard & Mann, 1979). In relatively sheltered locations, such as Wainui and Ohinepaka Bays, *Ecklonia* may benefit from allocating more resources to the stipe, forming a perennial storage organ for carbohydrate reserves such as mannitol and laminarin. In more exposed regions, such as Tory Channel, water movement is generally more intense. In such a situation, a long stipe is more likely to be broken, and a short, flexible stipe will confer an advantage (Norton *et al*, 1982). However, plants may need to allocate more resources to lamina production to compensate for the loss of storage potential. Similarly, plants in deep or low light environments may require greater storage reserves than plants in shallower locations (Lüning, 1979).

At a smaller scale, variation in *Ecklonia* morphology within Akaroa Harbour may result from differences in exposure between Wainui Bay and Ohinepaka Bay. Stipe length was significantly longer in Ohinepaka Bay, and may reflect the more sheltered aspect of this site. The evidence for this is mainly correlative, but it fits in with broader scale patterns described in *Ecklonia* populations elsewhere; short stiped varieties may be well adapted to wave exposure (Kirkman, 1981). *Ecklonia* from deep sites in northern New Zealand and from sheltered Fairlight Bay in New South Wales have very long stipes, compared to shallower and more exposed sites in Western Australia (Novaczek, 1981; Larkum, 1986; Hatcher *et al,* 1987).

The extent of morphological variation between the sites of my study was relatively small compared to the large variations in morphology over the range of *E. radiata* in New Zealand and Australia (Figure 19). A good indicator of the trend in regional morphology is the ratio between stipe-length and lamina-length. In mature plants, this ratio ranges from 0.74 in Wainui Bay to 1.03 in Ohinepaka Bay where plants generally have longer stipes (Table 3). Plants in Tory Channel generally have shorter stipes and longer lamina, giving a ratio of 0.59. In contrast populations of *E. radiata* in northern New Zealand have ratios of between 2.0 & 3.0, because of their long stipes (Novaczek, 1981). The stipe-length to lamina-length ratio of *E. radiata* in Australia ranges from 0.13 to 0.18 near Perth (Hatcher *et al*, 1987), to 2.67 in New South Wales (Larkum, 1986). This wide variation in morphology over the distribution of *E. radiata* has been attributed to environmental factors associated with depth,

wave exposure, and density (Novaczek, 1981; Larkum, 1986). Similar effects have also been described in species of *Laminaria* in the Northern Hemisphere (Chapman, 1973; Mann, 1971).

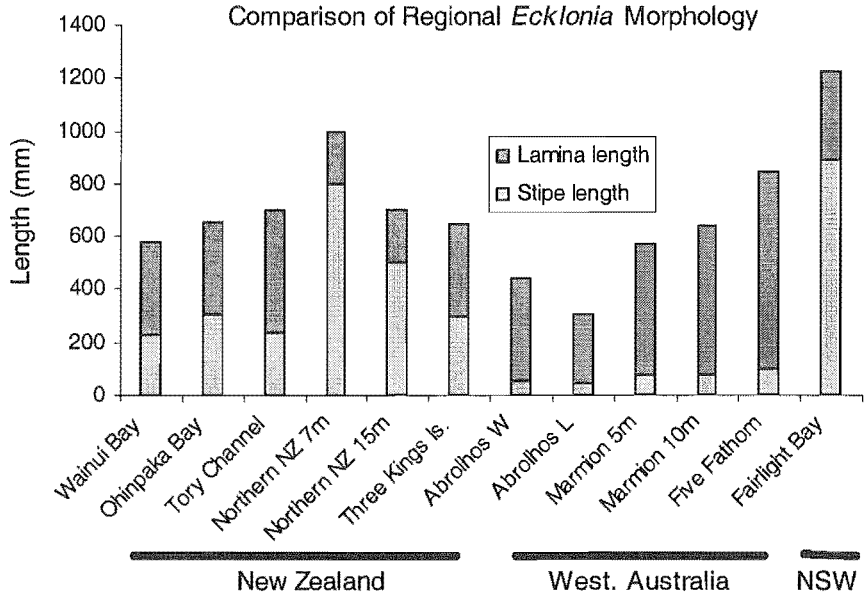

Figure 19. Morphological variability of mature *E. radiata* at sites in New Zealand and Australia. Data are from the present study and also Novaczek (1984c), Larkum (1986), Hatcher *et al* (1987).

Gross lamina growth did not differ between Wainui and Ohinepaka Bays, and therefore the difference found in net lamina growth suggests a higher rate of erosion at Wainui Bay than at Ohinepaka Bay (Figure 9). This may also reflect differences in exposure between these two sites, with Wainui Bay being more exposed than Ohinepaka Bay. Similarly, stipe growth rates were significantly higher in Ohinepaka Bay, which further suggests a high level of resource allocation to stipe size at this site.

More generally, the growth rates of *E. radiata* in this study were lower than those found in comparable studies elsewhere. Peak growth occurred during late spring, but seasonal fluctuations in growth were small. Mature plants displayed weak seasonal fluctuations in growth compared to *Ecklonia* in northern New Zealand (Figure 20). *Ecklonia* at 3m depth in Akaroa Harbour grew more slowly than *Ecklonia* at 7m depth in northern New Zealand (Figure 20). Furthermore, growth rates at 3m in Akaroa Harbour were of a similar magnitude to those found at 15m depth in northern New Zealand. The cause of the low growth in Akaroa Harbour may be related to light limitation by the *Macrocystis* canopy, water turbidity or both. However, other factors may also be involved, such as lower temperatures, daylength, differences in growth form, responses to water motion, and nutrient-depletion (Larkum,

1972; Norton *et al*, 1982). Similarly, Kirkman (1989) found the growth rate of *E. radiata* to be negatively correlated with depth, but stopped short of attributing reduced growth to reduced light levels alone. My experiments (Chapter 3) show that shading by *M. pyrifera* can suppress growth in *E. radiata*, but the roles of turbidity, temperature, and nutrients are less clear.

The peak lamina-elongation rate found in my study was 1.68mm.day^{-1} during spring (mean annual growth rate = 1.06mm.day^{-1}). This value is an order of magnitude less than that determined by Larkum (1986) for populations of *E. radiata* in New South Wales during peak growth in spring (17.1-19.6mm.day^{-1}) and is also considerably less than the minimum growth observed during late summer (7.6mm.day^{-1}). Only at the northern-most limit of its range in Western Australia does *E. radiata* grow at a rate comparable to that found in my study (peak = 1.5-2.0mm.day^{-1} in spring) (Hatcher *et al*, 1987). Further south, on Marmion Reef near Perth, mean annual lamina elongation rates ranged from 1.72-2.62mm.day^{-1}.

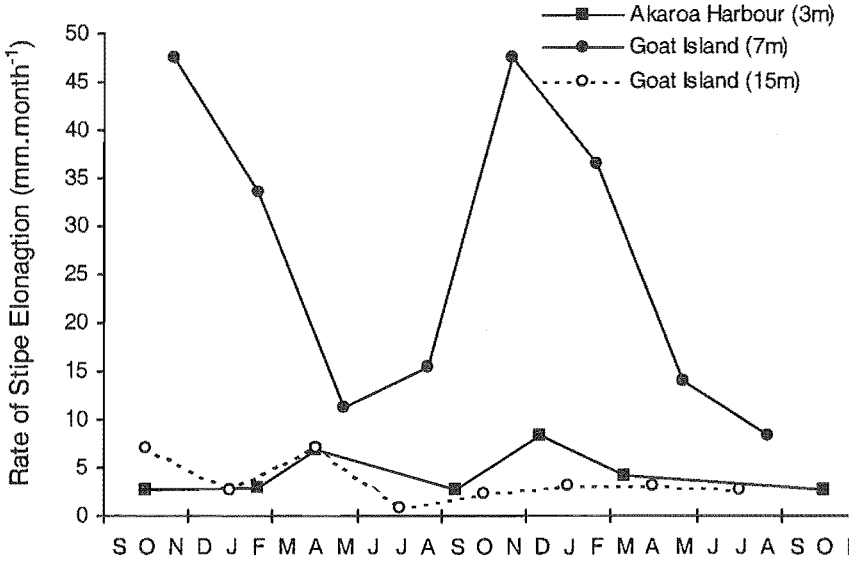

Figure 20. Comparison of stipe-elongation rate in *E. radiata* (with an initial stipe length of 150-500mm) between Akaroa Harbour (Wainui and Ohinepaka pooled) and Goat Island Bay, near Auckland. In northern New Zealand stipe-elongation rates of *E. radiata* peaked at ~48mm.month^{-1} at 7m depth, and ~7mm.month^{-1} in plants at 15m depth (Novaczek, 1984c). In comparison, mean daily growth peaked at ~8mm.month^{-1} in Akaroa Harbour at 3m depth.

The estimates of density, standing-stock and productivity obtained in this study are generally low in comparison to other studies throughout the range of *E. radiata* in Australia and New Zealand (Table 17). Mean densities were lowest at Tory Channel, where the high diversity of algal species may limit *E. radiata* abundance (Chapter 3). The low densities of mature *E. radiata* observed in this study, in comparison to other studies, may result from low

rates of recruitment and/or survival. Kirkman (1981) found the annual mean density of *Ecklonia* recruits in Western Australia to be ~3.0.m^{-2}. In comparison, the mean annual density of recruits in my study was typically less than 0.5.m^{-2} (Figure 14a). Mature *Ecklonia* in Kirkman's (1981) study were also more abundant than in my study (~22.m^{-2} vs. ~5.m^{-2}). A consequence of this low density is correspondingly low estimates of standing-stock and productivity (Choat & Schiel, 1982), which can give the impression that individual plants perform poorly in these situations. In contrast, the annual dry-weight production of individual *E. radiata* obtained was not especially low in comparison to estimates by other authors in northern New Zealand and Australia. Estimates of individual productivity in my study (54-88g.yr^{-1}) are generally higher than those found by Novaczek (1984c) in Goat Island Bay at 7m depth (48-59g.yr^{-1}) and 15m depth (20-47g.yr^{-1}), despite the comparatively low growth-rate of the plants in my study. This may reflect differences in morphology between these sites; plants at Goat Island generally have smaller laminae than those found in Akaroa Harbour, and allocation to lamina growth decreases as these plants get older (Novaczek, 1984c).

Table 17. Estimates of density, standing-stock, and productivity for *E. radiata* taken from the literature. *indicates that wet-weight estimates were converted to dry-weight using 1:7.14 ratio (Larkum, 1986). [1]indicates the peak in depth distribution from which density and standing stock were estimated.

Author	Location	Depth (m)	Density (No.m^{-2})	Standing stock ($kg_{dry}.m^{-2}$)	Production ($kg_{dry}.m^{-2}.yr^{-1}$)	Production per plant ($kg_{dry}.yr^{-1}$)
Kirkman (1984)	Aust Perth (Marmion Reef)	2-7	22.5	1.68*	2.9*	0.129*
Kirkman (1989)	Aust Perth (Marmion Reef)	2-5	24.5	1.82*	4.4	0.180
	Aust Perth (Marmion Reef)	10	11.5	0.70*	1.8	0.140
Larkum (1986)	Aust New South Wales	1.5	22.5	2.2	3.1	0.138
Hatcher *et al* (1987)	Aust Abrolhos W	2-5	0.62	0.037*	0.048*	0.076*
	Aust Abrolhos L	2-5	0.06	0.002*	0.002*	0.034*
	Aust Perth (Five Fathom Bank)	27	0.56	0.044*	0.056*	0.100*
Novaczek (1984c)	NZ Goat Island Bay	7	47.0	-	3.0	0.059
	NZ Goat Island Bay	15	16.0	-	0.4	0.047
Choat & Schiel (1982)	NZ Poor Knights Islands	11[1]	21	0.38	-	-
	NZ Goat Island Bay	11[1]	22	0.29	-	-
	NZ Little Barrier Island	11[1]	-	0.90	-	-
	NZ Owhiro Bay	5[1]	1.5	0.17	-	-
	NZ Three Kings Islands	18[1]	15	0.07	-	-
Schiel (1990)	NZ Fiordland	12	3	-	-	-
Present study	NZ Wainui Bay	3-4	6.25	0.26	0.208	0.054
	NZ Ohinepaka Bay	3-4	7.81	0.40	0.439	0.088
	NZ Tory Channel	4-5	1.74	0.07	-	-

Survival of new recruits in Akaroa Harbour was extremely variable and possibly affected by disturbance from water motion. Mortality among mapped recruits (≈25mm length) in Wainui Bay was 96% over two months, compared with only 28% in more sheltered Ohinepaka Bay. Overall survival rates of *E. radiata* in this study are comparable with those

found by other authors in northern New Zealand. Schiel and Choat (1980) found that mortality tended to vary with density, being 37%.yr^{-1} at 1.m^{-2} and 59% yr^{-1} at 45.m^{-2}. The mean annual mortality of all tagged plants in this study was 32.6%.yr^{-1} in Wainui Bay, 38.5%.yr^{-1} in Ohinepaka Bay, and ~55%.yr^{-1} at the more exposed Tory Channel site. Environmental factors, such as water movement, may exacerbate or directly affect mortality rates.

Mortality is not generally related to size, except in the smallest plants (<40g) in Ohinepaka Bay. Differences in survival found amongst a cohort of 47 juvenile *E. radiata*, further suggests a degree of size specific mortality in smaller plants. However, a potentially confounding factor is that, as plants grow, the lamina tends to reduce in size as the stipe lengthens, resulting in older plants with relatively low biomass. Stipe volume gives a clearer pattern, with plants with larger stipes having a greater risk of mortality. The strong relationship found between stipe volume and age (Figure 4), suggests that older plants generally have a greater mortality rate than younger plants. Mortality of *E. radiata* was related to age, and is a function of the condition of the stipe and its associated holdfast. Stipe-volume increases throughout life and is accompanied by loss of pliability and deterioration of the holdfast. Loss or damage to the stipe or holdfast will generally result in the death of the plant. In contrast, the plant will generally survive partial lamina loss. De Wreede (1986) noted that mortality in mature *P. californica* is probably the result of water motion, and affects larger/older plants to a greater degree. Water-motion that causes mortality in large plants may also cause less severe lamina loss in other individuals, reducing their biomass and also their future risk of mortality.

The maximum age obtained by *E. radiata* in this study was estimated from stipe-volume measurements and suggests that individuals may reach ages of ~7 years in Akaroa Harbour. This is comparable to the maximum age of 10 years found by Novaczek (1981) in Goat Island Bay, who suggested that even older plants might be present at depths of 18-20m.

Mature *E. radiata* in this study bore ripe sori year-round, but the greatest proportions of plants with full sori were present from late autumn to spring. Year-round spore production in laminarians is uncommon. Chapman (1984) described a population of *Laminaria digitata* in Nova Scotia that produced large numbers of spores throughout the year. Similarly, Novaczek (1984c) found that *E. radiata* bear sori, often ripe, year-round in populations in northern New Zealand, although these ripe sori generally did not release spores during summer.

Further work is required to determine if the populations of *E. radiata* in Akaroa Harbour do in fact release spores naturally year-round.

Mean spore density was estimated at up to 1.2 x 10^5 per cm^2 of sori. Thus recruitment is unlikely to be limited by spore availability, but more probably by the availability of suitable recruitment sites (Anderson *et al,* 1997; Kirkman 1981), and post-settlement mortality (Vadas *et al*, 1992). Recruits up to 10mm in length appear from mid-spring and grow to ~160mm over the course of a year. In northern New Zealand, *E. radiata* are reproductively fertile from May to November and recruitment of sporophytes generally occurs from September to December (Novaczek, 1984c).

This study supports the notion that schedules of mortality will tend to be more tractable in terms of age (stipe-volume) than biomass. Conversely, because sori area is generally proportional to lamina biomass, reproductive output will be more tractable in relation to biomass than age. Similarly, Chapman (1986) found that in *Laminaria longicruris*, size did not affect mortality, but was related to reproduction.

The predicted stable age-distributions at both Akaroa sites did not differ significantly from the average age-distributions observed at each site (Table 14). No such correspondence was found between predicted and average size-distributions at these sites (Table 11). This suggests that the age-structure of both populations is fairly stable over large time scales, but size-structure is not. Additionally, there was high variability in age- and size-structure through time at both sites, which is probably a reflection of highly variable recruitment at smaller scales. This is to be expected: population structure will only be stable when size- or age- specific schedules of fecundity, mortality, and growth remain constant (Aberg, 1992a).

The determination of age-structure in kelp populations generally requires the use of long-term tag and recapture regimes or destructive sampling methods (e.g. stipe-rings) (Novaczek, 1981; Kain, 1963; Chapman, 1986; Ang, 1991). Estimation of age-structure from size-structure has met with limited success due to the plasticity of many algal features (Grant, 1989; Russell, 1990; De Wreede, 1984; Chapman, 1986). Novaczek (1981) has suggested that stipe-length and stipe-diameter are unsuitable as determinants of age in *E. radiata* because of inconsistencies in the rate of stipe elongation with depth and wave exposure, and the slow rate of stipe-diameter growth. Similarly, Larkum (1986) examined a population of *E. radiata* from a sheltered location in New South Wales and found no correspondence between stipe-length and age. In this study I combined stipe-diameter and stipe-length to obtain a new parameter, stipe-volume, which displays good correspondence with known age.

Hymanson *et al* (1990) suggested that the presence of an overlying surface canopy, such as *M. pyrifera* in my study, might produce irregular growth patterns in understorey kelps. These irregularities, in turn, would make morphological features unreliable indicators of plant age. To test for such irregularities in the present study, mean annual growth in stipe-volume was compared between years, sites and initial size category. Annual growth in stipe-volume did not vary significantly between the three years of study ($p=0.553$). This result supports the use of stipe-volume as a proxy for age. The estimates of *E. radiata* age used in this study were validated for a period of up to three-years with plants of known age. Thus it was possible to construct viable age-distributions for *E. radiata* populations in Wainui and Ohinepaka Bays using a combination of methods, namely short-term tag and recapture and the correlation of known age with a derived parameter (stipe volume).

Whether or not to use age- or size-based demographic techniques depends on the questions being asked. Age-based techniques are useful in discerning features such as longevity, recruitment or mortality episodes, and turnover rates of stands. Size-based techniques address questions concerning domination of space, resource utilisation, and size-refuges. My study has demonstrated that age is an appropriate demographic parameter to use when dealing with stipitate laminarians such as *E. radiata*, and supports the suggestion that studies of organisms that potentially have age-specific and size-specific demographic schedules may benefit from a dual approach.

The results of this study suggest that environmental factors may influence patterns of morphology, density, biomass and growth in *E. radiata* in a similar manner to the effects observed in other laminarians (Sjötun *et al*, 1993). The mechanism behind this is still unclear; the observed size- and age-distributions in Akaroa Harbour may reflect environmental factors that affect distributions directly, by selectively removing specific size- or age- classes. For example, older plants may have a greater risk of being removed by adverse water motion due to poor holdfast condition (De Wreede, 1986). Alternately, site-specific conditions may illicit specific growth responses, such as shorter stipes or longer laminae. These two processes are likely to be interrelated at the population level, such that adaptive life-history traits are selected for, while ruinous traits are selected against. More work is required to discern the relative contributions of genetic differentiation versus phenotypic variability in *E. radiata* (Chapman, 1973).

The techniques used in this study to model the demography of *E. radiata* have several limitations. In particular, the techniques are likely to be specific to the populations studied.

Further work is required to test the widespread appropriateness of these techniques on other populations and over larger time scales.

This study used a number of assumptions to derive data for life tables and transition matrices. While these assumptions may be valid, they are by necessity simplifying, and will reduce the resolution of the models. Similarly, in many instances correlations were used to estimate variables such as biomass and reproductive output from measurements of *in situ* plants. Estimates of age derived from stipe volume are not true measures of age (such as from growth rings or following since recruitment), but only of apparent age. The deviation of apparent age from true age will be more severe in heterogeneous environments where there is large variability in vital rates between individuals of the same age. In such populations, the utility of age-based demographic techniques is diminished in favour of more conventional size-based methods. Also, there are limitations in the composite curve used to estimate plant age from stipe-volume. The curve represents the 'average' stipe growth of an average plant under constant conditions. Obviously, such conditions cannot be realised, and the curve is at best an approximation for any one plant.

Another crucial limitation of these techniques are problems associated with underrepresented age- or size-categories. A few highly variable individuals within a small category may unnaturally bias that category, and lead to unreliable conclusions. Similarly, the size of category chosen will also impact the results to a degree. Specifically, small new recruits (<20mm) were poorly represented in these demographic models. A consequence of this, for example, might be that the survival probabilities for the smallest categories will be overestimated due of a lack of data concerning the smallest individuals within that category.

Additionally, there are caveats associated with modelling the stable age/size structure of a populations with data obtained from short-term studies. In this study, transition probabilities were determined over three one-year periods, which may or may not accurately reflect actual transition probabilities. Similarly, the predictions of these models are only truly valid under ideal (constant) environmental conditions. This limits the generality of these models, and hence their utility, at larger temporal and special scales.

The assumptions of the stage-based Lefkovitch (1965) matrix model are naturally violated by most demographic studies. These assumptions relate to constancy of environmental conditions, unlimited space, and the absence of inter- and intraspecific interactions. Of significance to this study are the possible effects of density and the presence of *M. pyrifera.* Density related phenomena are unlikely to affect mature *E. radiata* at densities up to $\approx 45.m^{-2}$

(Schiel & Choat, 1980). Density effects on new recruits are potentially more severe, since their distribution is often clumped. The effects of density on recruits, and the influence of the *M. pyrifera* canopy are examined in subsequent chapters.

Chapter 3: Canopy Interactions

3.1 Introduction

Light-gaps through canopies are of considerable importance in both terrestrial and marine systems (Connell *et al*, 1997), representing important opportunities for understorey species and the propagules of canopy-forming species to grow and develop by the provision of light and space (Foster, 1975b; Underwood, 1992). Previous studies have demonstrated that light limitation is an important structuring factor in macroalgal communities (Kain, 1966; Gerard, 1984; Novaczek, 1984a; Santelices & Ojeda, 1984; Schiel & Foster, 1986; Maegawa *et al*, 1987; Kennelly, 1989; Kirkman, 1989; Luning, 1981). The low light levels found beneath algal canopies can inhibit the recruitment and growth of smaller canopy and understorey species (Edwards, 1998; Dayton *et al,* 1999; Graham *et al,* 1997).

Macrocystis canopies are particularly effective at pre-empting light through the occupation of space at the sea surface. These canopies often fluctuate greatly in biomass due to stochastic disturbance by hydrodynamic processes. These fluctuations can impact lower canopy layers substantially. For example, in California, thinning of the *Macrocystis* canopy during El Niño can result in enhanced growth of understorey blade-stage *Macrocystis* (Schroeter *et al*, 1995). Additionally, both Reed & Foster (1984) and Watanabe *et al* (1992), suggest that the persistence of many understorey species in Californian kelp forests is controlled by the frequency of storms that remove *Macrocystis* canopies.

It is generally held that the timing of light/space gaps relative to the reproductive periods of algae determines which species are available to occupy space (Dayton, 1975; Schiel, 1980; Reed *et al*, 1996). However, laboratory based studies suggest that laminarian gametophytes and small sporophytes can lie dormant under low light levels for extended periods (Kain, 1966; Novaczek, 1984a; Bolton & Levitt, 1985; Tom, 1993; Gerard, 1997). If this ability is realised in the field, propagules lying dormant beneath mature canopies will appear irrespective of reproductive seasonality (Kimura & Foster, 1984).

The kelp forests in sheltered embayments of Akaroa Harbour are dominated by *Macrocystis pyrifera,* which forms extensive canopies at the sea surface. These canopies overshadow understorey *Ecklonia* and reduce light levels considerably. However, over most of its distribution in northern New Zealand and Australia, *Ecklonia* is the dominant canopy forming alga, unshaded by other species, and often occurring in dense monospecific stands (Schiel & Choat, 1980). Plants from open habitats often show pronounced responses to shading (Stuefer & Huber, 1998) and the response of *Ecklonia* to low light levels has been well documented. For example, low light will generally result in reduced growth and reduced

reproductive output (Kirkman, 1989; Novaczek, 1984c). The response of southern *Ecklonia* to a *Macrocystis* canopy may mirror these studies. However, there may also be important distinctions; depth is not a good proxy for light, as many other factors also vary with depth, such as temperature, water motion, and nutrients (Schiel & Foster, 1986). Futhermore, the mean ocean temperature is generally cooler in southern New Zealand than in northern New Zealand or in Australia. This may result in a lower metabolic rate and a potentially lower light requirement in southern *Ecklonia*. Novaczek (1984a) has suggested that gametophytes of *E. radiata* from northern and southern sites in New Zealand have distinct optimal temperature ranges for growth and reproduction.

These factors alone are enough to suggest that southern New Zealand *E. radiata* populations may differ profoundly from northern New Zealand and Australian populations in their response to low light. Additional factors are that the surface *Macrocystis* canopy in Akaroa Harbour undergoes large fluctuations in biomass (Figure 3), undoubtedly resulting in large fluctuations in light levels beneath, and that light quality and quantity will be affected by the high turbidity of Akaroa Harbour. Furthermore, the effects of *Macrocystis* on understorey species in New Zealand may not mirror the findings of other studies because *Macrocystis* surface canopies are generally less dense in New Zealand than in homologous *Macrocystis* dominated communities overseas (Schiel & Nelson, 1990).

This study examines the interactions in a three-tiered kelp community consisting a surface *Macrocystis* canopy, an *Ecklonia* subcanopy, and an understorey assemblage of corallines and juvenile kelps. This system is relatively simple in comparison to other kelp communities consisting of multiple tiers and multiple species within tiers. The main hypothesis tested was that the *Macrocystis* and *Ecklonia* canopies suppress recruitment and growth of *Ecklonia* by occupying space and pre-empting light. This hypothesis was tested through a series of canopy and understorey manipulations. In particular, by examining the effects of the surface *Macrocystis* canopy on *E. radiata* over a spatial scale of 3km to 300km, and the effect of encrusting coralline on laminarian recruitment.

3.2 Methods

The canopy removal manipulations in this section are divided into three experimental series, outlined in Table 18. The first series of canopy removals had an orthogonal design involving the removal of *Ecklonia* and *Macrocystis* canopies to determine the effect of these layers on the recruitment, growth, and survival of juvenile *E. radiata*. The second series examined the effect of the surface *Macrocystis* canopy on the growth, survival and recruitment of *E. radiata* over a range of temporal and spatial scales. The third series examined the effect of the coralline substratum on recruitment of *E. radiata*, in addition to the influence of overlying macroalgal canopies. These series are described in more detail in later sections.

Table 18. Experimental designs "±*E. r*" = presence/absence of *Ecklonia*, "±*M. p*" = presence/absence of *Macrocystis*, "±*M. p*" canopy = presence/absence of surface canopy, "±Can." = presence/absence of macroalgal canopy, "±Sub." = presence/absence of coralline substrate. Dates in bold indicate treatment installation, sampling periods are also indicated.

Series		Design	n	Site	Dates	Size	Testing
I	a	+ *E. r* + *M. p*	5	Wainui Bay	**Spr95**, Sum95, Win96, Spr96, Sum97, Spr98	2 x 2m	Effect of individual canopy layers on recruitment, growth, and mortality.
		+ *E. r* − *M. p*	5				
		− *E. r* + *M. p*	5				
		− *E. r* − *M. p*	5				
	b.	+ All canopies	5	Wainui Bay	**Spr95**, **Spr96**, **Sum97**, **Aut98**, Spr98	2 x 2m	Canopy recovery, timing of removal
		− All canopies (x4)	5				
II	a.	+ *M. p* canopy	5	Wainui Bay	**Spr95**, **Sum95**, Win96, Spr96, Sum97, Spr98	2 x 2m	Presence / absence of surface canopy on recruitment, growth, mortality (continual).
		− *M. p* canopy (once)	5				
		− *M. p* canopy (cont.)	5				
	b.	+ *M. p* canopy	2	Cape Three Points	**Win97**, Spr97, **Sum98**, Spr98	10 x 2m	Presence / absence of surface canopy on recruitment, growth, mortality
		− *M. p* canopy (A)	2				
		− *M. p* canopy (B)	2				
	c.	+ *M. p* canopy	2	Tory Channel	**Aut98**, Spr98	5 x 5m	Presence / absence of surface canopy on recruitment, growth, mortality.
		− *M. p* canopy	2				
III	a.	+Can. +Sub.	5	Wainui Bay	**Spr96**, Aut97, Aut98, Spr98	15 x 15cm	Effect of coralline substrate and macroalgal canopy on recruitment (presence of dormant propagules).
		+Can. −Sub.	5				
		−Can. +Sub.	5				
		−Can. −Sub.	5				

Throughout this study, 'recruitment' and 'new recruits' refer to the appearance of laminarians (*Ecklonia* and *Macrocystis*) ≤60mm (total length) within treatments. Only plants >60mm could be reliably identified to species and these were then classified as juveniles of a particular species. Size is closely correlated with maturity in *E. radiata* (Chapter 2), hence I classed juvenile *Ecklonia* as ranging from 60-250mm in total length. Mature *Ecklonia* were classed as any individual >250mm in total length. Juvenile *Macrocystis* were classed as any individual <1m in total length. *Macrocystis* >1m in total length were classed as mature.

Mature *Macrocystis* were further categorised as either 'subcanopy' or 'canopy-forming', depending on whether the plant reached the sea surface and formed a canopy. Canopy-forming plants were generally longer than 3m.

Plants were tagged using Dymo™ tape as described in Chapter 2 (section 2.2.1.1). An attempt was made to always tag juvenile plants, but this size class was not always present within treatment areas. As a result, growth rates cannot be directly compared across time-intervals because tagged plants were often of different sizes. *Ecklonia* and *Macrocystis* were removed by cutting through the stipe just above the holdfast to avoid disturbing the substratum. Partial removals of *Macrocystis* (just the surface canopy) were performed by cutting to a depth of 1m during low tide, leaving subcanopy fronds intact.

3.2.1 Series I – Orthogonal Canopy Removals

In Spring 1995 an orthogonal canopy removal experiment was installed in the kelp forest of Wainui Bay (Figure 2). Four treatments (n=5) were done, covering all combinations of *Ecklonia* and *Macrocystis* canopy removal (Table 18, Series Ia). Only mature *Ecklonia* were removed, leaving behind 4.1 ± 0.7 juvenile (<250mm) *Ecklonia* in each 2m x 2m replicate, too few to produce any density effects. Treatment areas were surveyed prior to manipulation and at approximately quarterly intervals for one year and at less regular intervals for two more years (Table 18, Series Ia). Particularly foul weather and poor underwater visibility prevented regular sampling during the second year. The numbers of recruits, juvenile and mature *E. radiata* were counted within each treatment area. Up to five juvenile *E. radiata* were tagged and their total-length measured within each replicate. All other algal species present were also counted. All experimental plots were randomised within the kelp forest, which was approximately 400m x 90m in area.

Canopies will eventually recover, so at some stage there is no longer any effect of canopy removal. For this study, the abundance of *Macrocystis* fronds in each quadrat was used as an indicator of a continued *Macrocystis* effect. Natural fluctuations in the *Macrocystis* canopy of Wainui Bay were assessed by removing the *Macrocystis* canopy from a known area (2 x 2m) of kelp forest to a depth of 1m at approximately seasonal intervals. The removed canopy was drained and then wet-weighed. The persistence of the *Ecklonia* removal effect was assessed in relation to the abundance of mature (>250mm) plants.

Another facet of series I was the periodic removal of all canopy layers from additional 2 x 2m treatment areas. These were repeats of the original *–E. r –M. p* treatment, performed on three subsequent occasions over the course of ~30 months (Table 18, series Ib). The

abundance of new recruits, juvenile and mature *E. radiata* within these quadrats during spring 1998 was used to assess the recovery of the *E. radiata* understorey.

3.2.2 Series II – Macrocystis Canopy Removal

To assess the impact of the *Macrocystis* surface canopy on the recruitment, growth and survival of *E. radiata* at different temporal and spatial scales, three canopy removal experiments were set up in Wainui Bay, Cape Three Points, and Tory Channel (Table 18, Series II). At all sites, at least two treatments were installed; removal of the surface *Macrocystis* canopy to a depth of 1m (*–M. p* canopy), and a control in which no canopy was removed (*+M. p* canopy). Different experimental protocols were followed at each site because these experiments were run in conjunction with *Macrocystis* canopy harvesting trials (Pirker, PhD thesis), which, through logistic necessity, dictated the size, shape and extent of canopy removals.

At Wainui Bay an additional treatment, the continual removal of *Macrocystis* canopy, was installed in summer 1996 to gauge the effect of persistent canopy gaps (Table 18, Series IIa). At Cape Three Points an additional canopy removal, identical to the first, was performed in summer 1998 to gauge temporal effects of *Macrocystis* canopy removal (Table 18, Series IIb). At all sites at least 5 of the smallest *Ecklonia* within each replicate were measured and tagged. At Wainui Bay, all *Ecklonia* and other algal species were counted within each 2 x 2m treatment area. At Cape Three Points and Tory Channel, the number and size class of *Ecklonia* and abundance of other algae were surveyed within $1m^2$ quadrats (n=5) randomly placed in each treatment area.

3.2.3 Series III – Substrate Clearances

The primary rock cover within the kelp forest at Wainui Bay is a thick encrusting coralline alga (Plate 2). To test if this inhibited kelp recruitment, and if any effects depended on the presence of an overlying macroalgal canopy, orthogonal substratum and canopy removal treatments (n=5) were installed during spring 1996 at the Wainui Bay site (Table 18, Series III). One replicate of each substrate removal treatment was installed within an appropriate replicate of Series Ib (+canopy = *+M. p +E. r*, –canopy = *–M. p –E. r* in spring 1996). Each substrate clearance measured 15 x 15 cm. All traces of coralline algae were removed from the substrate using a cold chisel. Percent cover of coralline algae, numbers of kelp and other algal recruits, and sessile and sedentary invertebrates were counted on four occasions over 2 years.

3.2.4 Environmental Parameters

Levels of photosynthetically active light were measured using a Li-Cor quantum light meter at midday on 16 May 1997 at the Wainui and Ohinepaka Bay sites. Measurements (n=2) were performed at the surface, a depth of 1m (no canopy), a depth of 3m (no canopy), and beneath an *Ecklonia* canopy to assess the degree of light attenuation in these situations.

Sea-surface and bottom (depth = 3m) temperatures at the Wainui Bay site were measured with Onset™ temperature probes set to record at intervals of 36 minutes from December 1996 to May 1998. Temperature readings were converted into monthly averages. Air temperature and rainfall data for Akaroa Township from 1995 to 1998 were obtained from meteorological records published by the National Institute of Water and Atmospheric Research (NIWA).

The extensive turbidity of the water in Akaroa Harbour prompted the installation of sediment traps to gauge the influence of algal canopies on the accumulation of sediment on the substratum below. A 'station' consisted of two open jars (∅ = 40mm, height = 119mm) attached vertically to the substratum. Four stations were placed within the kelp forest at Wainui Bay, two of which were beneath an *Ecklonia* and *Macrocystis* canopy and two in areas where both canopies were continually removed. The sediment traps were removed and replaced five times between January and September 1998. The amount of sediment collected within each trap was measured, and expressed in terms of $mm.month^{-1}$.

3.2.5 Analysis

Data from series I and IIa were analysed as two-way ANOVA and ANCOVAs. Data from Cape Three Points and Tory Channel were analysed as nested ANOVAs (counts) or ANCOVAs (growth), with treatment areas nested within treatments. The three canopy removal sites in Series II (Wainui Bay, Cape Three Points, Tory Channel) were analysed separately, differences between these sites cannot be tested across all spatial and temporal scales due to differences in experimental protocol. Comparisons between these sites are limited to assessment of general effects of *Macrocystis* canopy removal. Data were transformed as required to meet assumption of normality. Post hoc tests (Tukey's HSD test) were performed on significant results ($p<.05$) to determine which treatments were significantly different.

Growth rates of tagged plants were calculated as the change in total plant length between census dates and expressed in $mm.day^{-1}$. Growth rate and survival data from Tory Channel were analysed as one-way ANOVAs. Abundance data were analysed as two-way ANOVAs,

using time and canopy treatment as independent variables. Replicate plots were pooled giving 10 random quadrats per treatment, and 10 tagged *E. radiata* per treatment.

Recruitment of algae within substrate clearances (series III) was analysed as a two-way ANOVA with replication at each sampling date, using the presence/absence of canopy and coralline as independent variables. Changes in the percent cover of coralline were analysed as repeated measures univariate and multivariate ANOVAs on arcsine transformed data.

3.3 Results

3.3.1 Series Ia - Orthogonal Canopy Removal

3.3.1.1 Recruitment

Removal of the *Macrocystis* and *Ecklonia* canopy at just a single time was not found to have a significant effect on the abundance of newly recruited laminarians appearing within treatment areas (Figure 21, Table 19). Recruitment did, however, differ significantly between years. Numbers of recruits peaked in spring and summer in both 1995/96 and 1996/97, and were also observed during spring 1998, suggesting a regular schedule of recruitment. Post hoc comparison indicated that recruits were more abundant in spring 1995 than in either spring 1996 or spring 1998. The identity of recruits could not be assessed at small sizes, but subsequent samples of juveniles suggest that the 1995/96 episode was primarily *E. radiata* (Figure 22) and the 1996/97 episode was primarily *M. pyrifera* (see later Figure 33a).

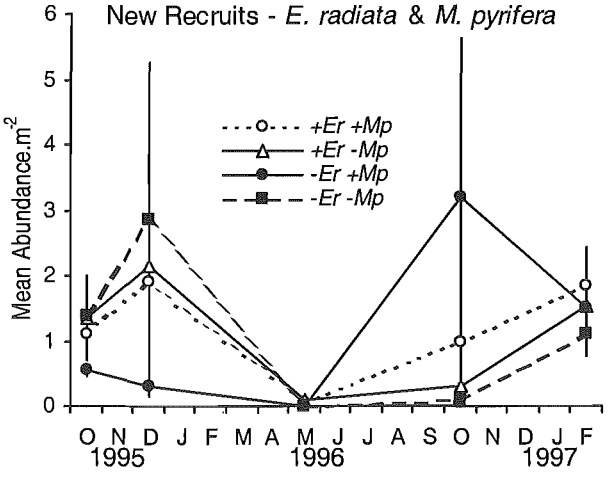

Figure 21. Mean abundance of new recruits within canopy removal experiment through time ± 1SE. *Mp* = *Macrocystis pyrifera*, *E.r* = *Ecklonia radiata* (spring 1998 not shown).

Table 19. Three-way ANOVA results for orthogonal once-only canopy removal performed in spring 1995. Fixed factors were canopies (+*Macrocystis*, –*Macrocystis*, +*Ecklonia*, –*Ecklonia*), year was a random factor (1995, 1996, 1998). The dependent variable was mean abundance.m^{-2} of new recruits present during spring in each year.

Effect	df	MS	F	p
Macrocystis Canopy	1,2	0.344	1.683	0.324
Ecklonia Canopy	1,2	0.235	0.450	0.572
Year	2,48	4.438	5.808	0.006**
Macrocystis x *Ecklonia*	1,2	0.214	0.232	0.678
Macrocystis x Year	2,48	0.204	0.268	0.766
Ecklonia x Year	2,48	0.522	0.683	0.510
Macrocystis x *Ecklonia* x Year	2,48	0.924	1.210	0.307

3.3.1.2 *Juvenile Abundance*

A delay was seen in the response of juvenile *E. radiata* to canopy removal; no effect was observed until winter 1996 (Table 20, Table 21). At this time, significant differences were due to the presence or absence of the *E. radiata* canopy (Figure 22, Table 22). The greatest number of juvenile *Ecklonia* were found in plots where both canopy layers were removed (*-E.r –M.p*). This treatment also displayed greater variation in the abundance of juveniles, suggesting that some plots had higher levels of recruitment. The juveniles found in these treatments had grown from the new recruits present in summer 1996, but the increase in abundance over and above the numbers of recruits previously present, also suggests that previously unsampled (perhaps microscopic) individuals had grown to >60mm length in approximately 5 months. There was no increase in the numbers of juvenile *E. radiata* in treatments in which *E. radiata* canopy was not removed.

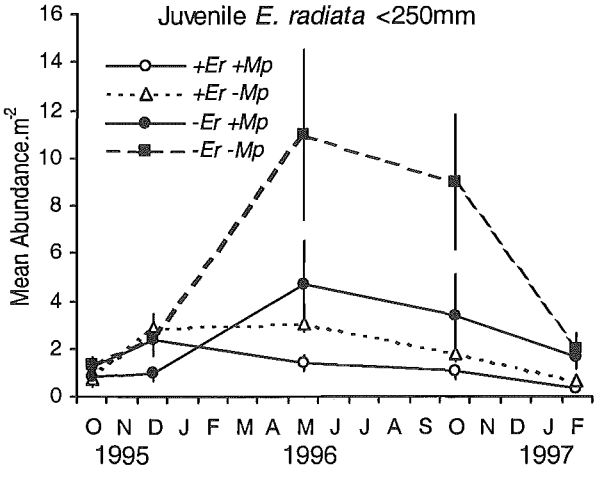

Figure 22. Mean abundance ± 1SE of juvenile *E. radiata* (<250mm total length) within orthogonal once-only canopy removal experiment. *+E. r/+M. p* = intact canopy layer, *-E. r/-M. p* = canopy layer removed (spring 1998 not shown).

By spring 1996, in addition to the continuing enhancement of *Ecklonia* recruits due to *Ecklonia* canopy removal, there was a significant response due to the removal of the *Macrocystis* canopy; the numbers of juvenile *Ecklonia* was greater in treatments where *Macrocystis* had been removed (Figure 22, Table 23). By summer 1997, the treatment effect had diminished as plants had outgrown the 60-250mm size category and the overshadowing canopy had recovered. Even so, there were still significantly more juveniles in *Ecklonia* removal treatments, and overall treatment rankings were the same as winter 1996 (Table 24). On the final survey in spring 1998 (October), the effect of *E. radiata* canopy removal had diminished (Table 25). However, at this time there was a moderately significant effect due to *Macrocystis* canopy removal, with slightly more juvenile *E. radiata* in *+Macrocystis* treatments (~0.83.m^{-2}) than in *–Macrocystis* treatments (~0.45.m^{-2}).

Table 20. *E. radiata* Juveniles: October 1995

Effect	df	MS	F	P
Macrocystis Canopy	1	0.001	0.002	0.960
Ecklonia Canopy	1	0.088	0.136	0.717
Macrocystis x *Ecklonia*	1	1.792	2.744	0.117
Error	16	0.653		

Table 21. *E. radiata* Juveniles: December 1995

Effect	df	MS	F	P
Macrocystis Canopy	1	76.05	2.804	0.113
Ecklonia Canopy	1	68.45	2.524	0.132
Macrocystis x *Ecklonia*	1	22.05	0.813	0.381
Error	16	27.13		

Table 22. *E. radiata* Juveniles: May 1996

Effect	df	MS	F	P
Macrocystis Canopy	1	2.247	4.420	0.052
Ecklonia Canopy	1	3.668	7.214	0.016*
Macrocystis x *Ecklonia*	1	0.063	0.123	0.729
Error	16	0.508		

Table 23. *E. radiata* Juveniles: October 1996

Effect	df	MS	F	P
Macrocystis Canopy	1	2.186	5.856	0.028*
Ecklonia Canopy	1	4.168	11.17	0.004**
Macrocystis x *Ecklonia*	1	0.518	1.387	0.256
Error	16	0.373		

Table 24. *E. radiata* Juveniles: February 1997

Effect	df	MS	F	P
Macrocystis Canopy	1	1.344	1.594	0.225
Ecklonia Canopy	1	7.184	8.518	0.010*
Macrocystis x *Ecklonia*	1	0.042	0.050	0.827
Error	16	0.843		

Table 25. *E. radiata* Juveniles: October 1998

Effect	df	MS	F	P
Macrocystis Canopy	1	2.370	4.809	0.043*
Ecklonia Canopy	1	0.191	0.388	0.542
Macrocystis x *Ecklonia*	1	0.003	0.006	0.941
Error	16	0.493		

Table 20 - Table 25. Two-way ANOVA results for orthogonal once-only canopy removal performed in October 1995. Fixed factors are canopies (*+Macrocystis*, *-Macrocystis*, *+Ecklonia*, *-Ecklonia*). The dependent variable was mean abundance ($m.^{-2}$) of <250mm *E. radiata* at the time of canopy removal, and at five subsequent times. Transformations were performed where appropriate to normalise data. * denotes significance at $p<0.05$, ** denotes significance at $p<0.01$.

3.3.1.3 Growth

The growth of tagged *Ecklonia* was affected by the removal of overlying macroalgal canopies. The *Macrocystis* canopy had the greatest effect on the growth rate of tagged *Ecklonia* during the initial period from spring 1995 to summer 1996 (Figure 23a; Table 26). The slowest growth rate over this period was seen in the treatment where both canopies were left intact (*+E. r +M. p*). The fastest growth rate was where *Macrocystis* was removed but *Ecklonia* left intact (*+E. r –M. p*). The anomalous result is that removal of both canopies (*-E. r –M. p*) produced lower growth rates than in the partial canopy removal treatments (*+E. r –M. p*, *–E. r +M. p*) resulting in a significant interaction term between the effect of *Ecklonia* and *Macrocystis* canopies on growth rate (Table 26).

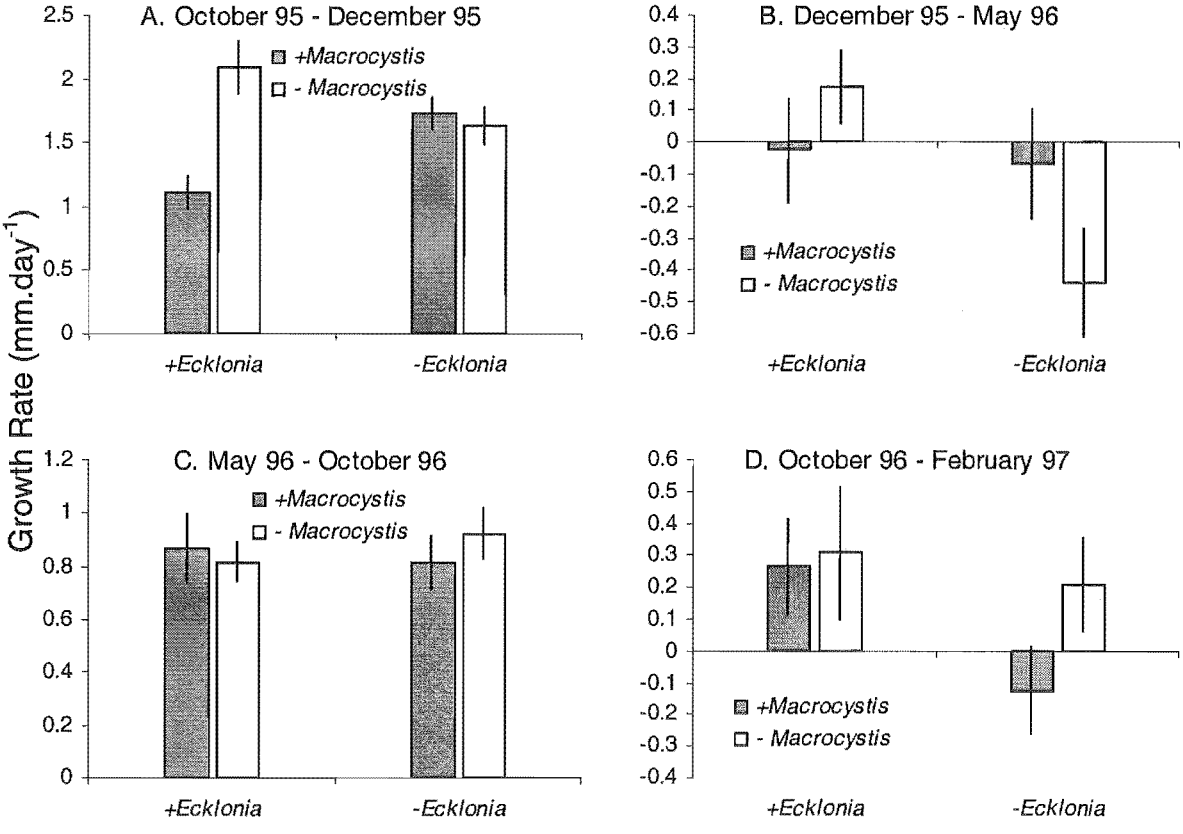

Figure 23 A-D. Mean growth rate (mm.day^{-1} total length) of tagged *E. radiata* within the once-only orthogonal canopy removal experiment over contiguous periods from initiation in October 1995 to February 1997 ± 1SE. *+Ecklonia/+Macrocystis* = intact canopy layer, *–Ecklonia/–Macrocystis* = canopy layer removed.

During the period between summer 1996 and winter 1996 growth rate was generally poor and varied between –0.4mm.day^{-1} and 0.2mm.day^{-1} (Figure 23b; Table 27). There was a significant interaction between *Macrocystis* and *Ecklonia* canopy removals; where growth was greatest in the absence of *Macrocystis* but only when *Ecklonia* was present. In addition, mean negative growth occurred in some treatments as a result of lamina erosion. The highest

rate of lamina erosion was observed in the complete canopy removal treatment (*–E. r –M. p*). The next highest erosion rate occurred in the *Ecklonia* only removal treatment (*–E. r +M. p*). In treatments where negative growth was observed, plants were generally covered in a layer of sediment.

Over the period from winter to spring 1996, there was no significant difference in growth between treatments; all treatments produced high growth rates of between 0.8 to 0.9 $mm.day^{-1}$ (Figure 23c, Table 28). Finally, the growth rate of *Ecklonia* was uniformly slow ($-0.15mm.d^{-1}$ to $+0.35\ mm.d^{-1}$) in all treatments over the period from spring 1996 to summer 1997, and there was no significant difference between treatments (Figure 23d; Table 29).

Superimposed on this experiment was the natural cycle of expansion and contraction of the *Macrocystis* canopy. By late winter/early spring 1996, the *Macrocystis* canopy was severely reduced in extent by winter storms, and was generally absent over summer 1997 (Figure 24a). It is expected that *Macrocystis* canopy effects would be reduced at this time. By summer 1997 the effect of *Macrocystis* removal had effectively ceased due to a reduction in frond density in *+E. r +M. p* and *–E. r +M. p*, and recovery in *+E. r –M. p* and *–E. r –M. p* (Figure 24b) ($F_{(3,16)}$=1.123; p=.368). Subsequently, a general pattern of high canopy biomass during winter and low canopy biomass during summer was observed from summer 1997 to winter 1998 (Figure 24a).

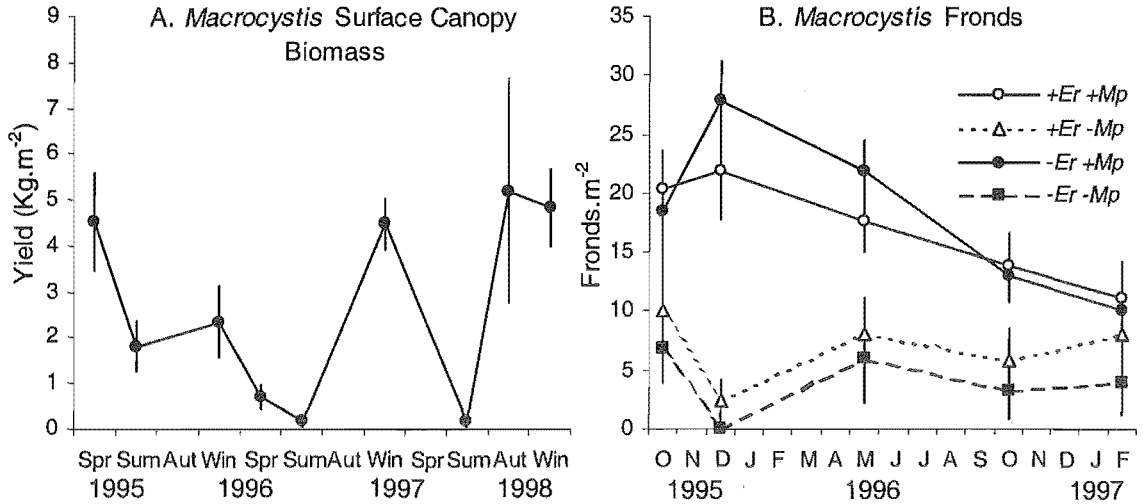

Figure 24 A – B. Indication of continued effect of *M. pyrifera* canopy removal. This was assessed in terms of (a) surface canopy biomass and (b) *Macrocystis* frond density.

Table 26. *E. radiata* growth rate: October to December 1995

Effect	df	MS	F	p
Macrocystis Canopy	1	4.061	8.6832	0.004**
Ecklonia Canopy	1	0.246	0.5251	0.471
Macrocystis x *Ecklonia*	1	3.662	7.8307	0.007**
Error	54	0.467		
	Tukey's HSD:	(+M.p +E.r) v. (+M.p –E.r) = 0.028*		
		(+M.p +E.r) v. (–M.p +E.r) = 0.000*		

Table 27. *E. radiata* growth rate: December 1995 to May 1996

Effect	df	MS	F	p
Macrocystis Canopy	1	0.000	0.0016	0.968
Ecklonia Canopy	1	1.943	6.9245	0.001**
Macrocystis x *Ecklonia*	1	2.636	9.3969	0.003**
Error	54	0.281		
	Tukey's HSD:	(–M.p +E.r) v. (–M.p –E.r) = 0.024*		

Table 28. *E. radiata* growth rate: May to October 1996

Effect	df	MS	F	p
Macrocystis Canopy	1	0.008	0.0381	0.845
Ecklonia Canopy	1	0.008	0.0363	0.849
Macrocystis x *Ecklonia*	1	0.089	0.4176	0.520
Error	54	0.214		

Table 29. *E. radiata* growth rate: October 1996 to February 1997

Effect	df	MS	F	p
Macrocystis Canopy	1	0.026	1.3483	0.250
Ecklonia Canopy	1	0.068	3.4857	0.066
Macrocystis x *Ecklonia*	1	0.002	0.0894	0.766
Error	54	0.019		

Table 26 - Table 29. Two-way ANCOVA results for orthogonal once-only canopy removal performed in October 1995. Fixed factors are canopies (*+Macrocystis, -Macrocystis, +Ecklonia, –Ecklonia*). The variable was growth rate (mm.day^{-1} total length) of tagged *E. radiata,* over four periods subsequent to canopy removal. Initial length was used as covariate. Tukey's Honest Significant Difference (HSD) test is included where appropriate (*M.p = Macrocystis pyrifera, E.r = Ecklonia radiata*). Transformations were performed where appropriate to normalise data. * denotes significance at p<0.05, ** denotes significance at p<0.01.

3.3.1.4 Mortality

The mortality rate of tagged *Ecklonia* within canopy removal treatments was assessed over two months from spring 1995 to summer 1996, and over 16 months from spring 1995 to summer 1997. There was no significant effect of canopy removal treatments on the mortality rate of *Ecklonia* over the initial two month period, although there was a higher average mortality in treatments where both canopies were removed ($F_{(1,16)}$=.897; p=.358) (Figure 25a). This may reflect the increased exposure of these plants (water motion, fish, sediment etc) following canopy removal. Over the longer 16 month period all treatments had similar rates of mortality ($F_{(1,16)}$=.001; p=.974) (Figure 25b).

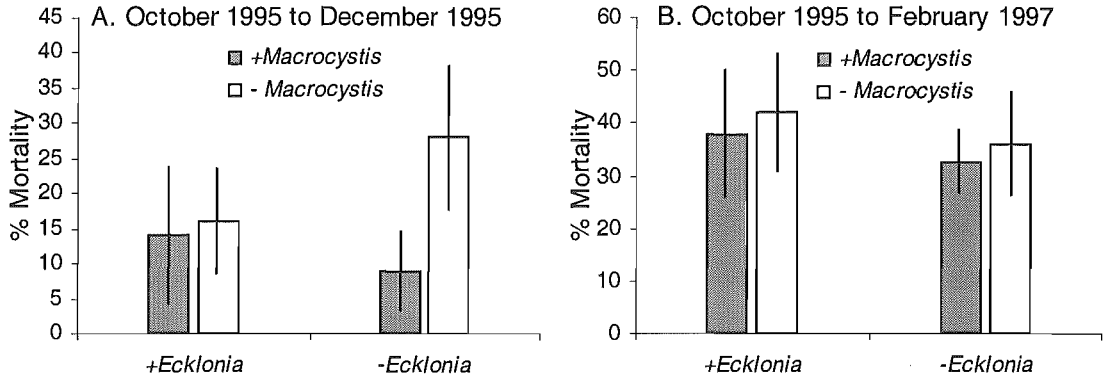

Figure 25 A-B. Percentage mortality ± 1SE of tagged *E. radiata* following once-only orthogonal canopy removal over (A) short-term and (B) long term after initiation in October 1995. *+Ecklonia/+Macrocystis* = intact canopy layer, *-Ecklonia/-Macrocystis* = canopy layer removed.

3.3.1.5 Mature Ecklonia *Abundance*

The abundance of mature *Ecklonia* displayed a dramatic recovery following removal from *–E. r +M. p* and *–E. r –M. p* in spring (October) 1995 (Figure 26). By spring (October) 1996, there was no significant difference between treatments ($F_{(3,16)}$=3.23; p=.054). Recovery of the *E. radiata* subcanopy was fastest in the treatment where both *Macrocystis* and *Ecklonia* canopies had been removed. By summer (February) 1997 the abundance of mature *E. radiata* was significantly greater in *–E. r –M. p* than in *–E. r +M. p* ($F_{(1,8)}$=11.61; p=.009).

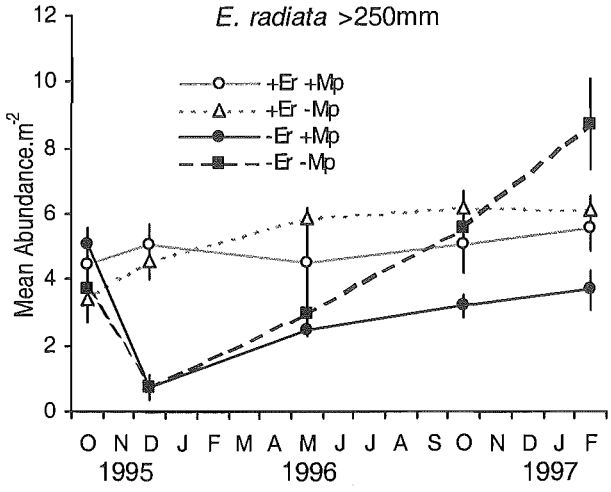

Figure 26. Mean abundance ±1SE of *E. radiata* >250mm within orthogonal once-only canopy removal experiment. *+E. r/+M. p* = intact canopy layer, *–E. r/–M. p* = canopy layer removed. October 1995 sample represents pre-removal abundance.

3.3.2 Series Ib – Recovery of Ecklonia *following canopy removal*

By spring 1998 there was no significant difference in the number of new recruits (Figure 27a) present in all total canopy removal treatments or the control ($F_{(4,20)}$=1.24; p=.327), however there was a trend for more recruits in more recently added treatments (Figure 27a). The numbers of juvenile *E. radiata* within *–E. r –M. p* treatments showed a significant difference during spring 1998 ($F_{(4,20)}$=4.96; p=.006) (Figure 27b); significantly more juveniles were present at 24 months than at 36 months or in the control (Tukey's HSD test <.05). The abundance of mature (>250mm) *E. radiata* generally increased with time since removal, and was significantly greater after 36 months than after 7, 20, or 24 months ($F_{(4,20)}$=14.7; p<.000) (Tukey's HSD test <.05).

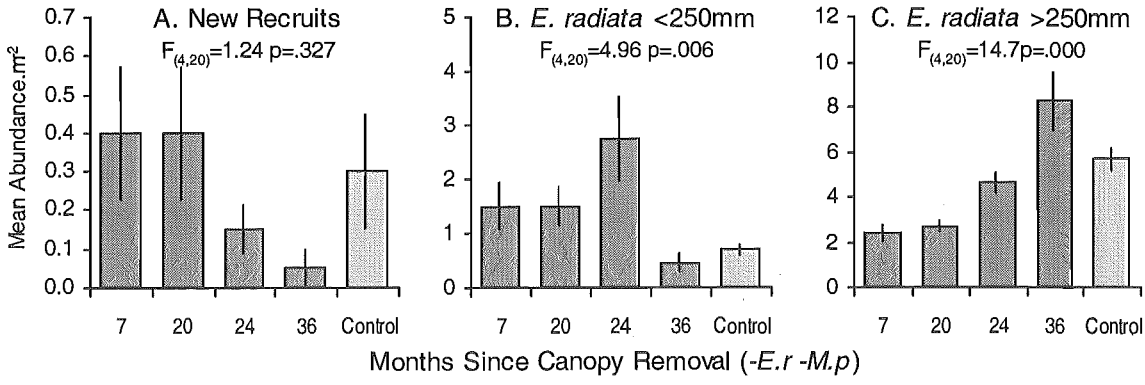

Figure 27 A-C. Mean abundance of three size classes of *E. radiata* within 4 identical canopy removal treatments (*-E. r –M. p*) performed at different intervals before sampling in spring 1998 ± 1SE. Numbers along the x-axis represent the number of months beforehand that treatments were installed. Control = *+E. r +M. p*.

3.3.3 Series II - Macrocystis *Surface Canopy Removal*

3.3.3.1 Recruitment

In Wainui Bay the abundance of recruits did not differ significantly between canopy removal treatments (including continual canopy removal) at sampling dates when recruits were present: spring 1995 ($F_{(1,8)}$=1.42; p=.26), summer 1996 ($F_{(2,12)}$=1.45; p=.27), spring 1996 ($F_{(2,12)}$=.32; p=.73), summer 1997 ($F_{(2,12)}$=.09; p=.91), spring 1998 ($F_{(2,5)}$=.82; p=.46) (Figure 28a). At Cape Three Points, a large recruitment episode occurred during early summer 1998 (Figure 28b). Although the abundance of recruits did not differ significantly between canopy removal treatments (when recruits were present) during summer 1998 ($F_{(2,3)}$=7.516; p=.07), or spring 1998 $F_{(2,3)}$=3.62; p=.159). The abundance of new recruits in Tory Channel was very low over the period of study (autumn to spring 1998) and they were absent from many replicates. No statistical test was performed.

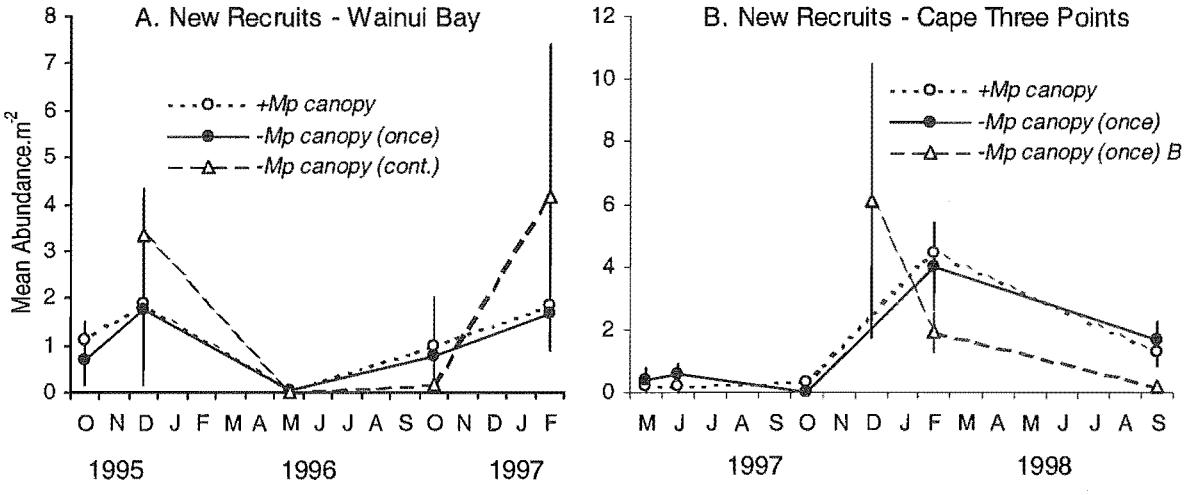

Figure 28 A-B. The abundance of newly recruited laminarians (<60mm) within treatment areas ±1SE at Wainui Bay and Cape Three Points. +*M. p* canopy = control, –*M. p* canopy (once) = surface *Macrocystis* canopy removed once, –*M. p* canopy (cont.) = continual canopy removal (Wainui).

3.3.3.2 Growth

Growth of tagged plants in Wainui Bay was enhanced by *Macrocystis* canopy removal over the initial period from spring 1995 to summer 1996 ($F_{(1,36)}$=9.842; p=.003) (Figure 29a). Over subsequent periods from summer 1996 to summer 1997, there was no significant difference between treatments, including the continuous canopy removal treatment: summer - autumn 1996 ($F_{(2,45)}$=2.44; p=.10)l; winter - spring 1996 ($F_{(2,53)}$=.12; p=.88); spring 1996 – summer 1997 ($F_{(2,48)}$=.62; p=.54).

At the Cape Three Points, the growth rate of tagged *Ecklonia* did not differ significantly between canopy removal treatments at any time (p>.05) (Figure 29b), but there were

significant differences in growth rate between transects within treatments during spring 1997 to summer 1998 ($F_{(2,3)}$=3.98; p=.022), and during summer 1998 to spring 1998 ($F_{(2,3)}$=4.83; p=.011), indicating that treatment placement had a greater effect than treatment itself. In Tory Channel, *Macrocystis* canopy removal had no significant effect on the growth rate of *Ecklonia*. Tagged *Ecklonia* grew at a rate of 0.40 to 0.50mm per day in both treatments from autumn to spring 1998. There was no significant difference between the control and the canopy removal treatment ($F_{(1,15)}$=.448; p=.513).

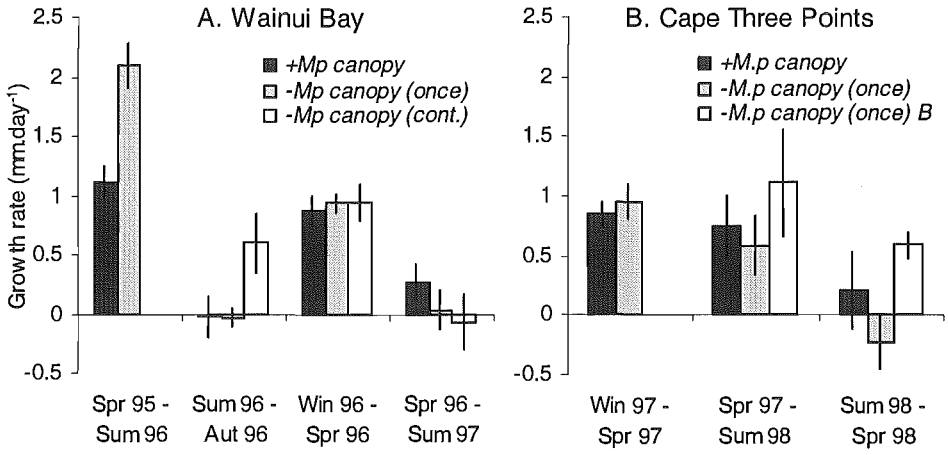

Figure 29 A-B. Growth rate of tagged *E. radiata* within control and within canopy removal treatments performed at A) Wainui Bay and B) Cape Three Points ±1SE. *+M. p* canopy = control, *–M. p* canopy (once) = surface *Macrocystis* canopy removed once, *–M. p* canopy (cont.) = continual canopy removal (Wainui).

3.3.3.3 Juvenile Abundance

The abundance of juvenile *Ecklonia* (<250mm) in Wainui Bay did not differ significantly between treatments at all sampling occasions between October 1995 and October 1998; (P>.05) (Figure 30a). Similarly, at Cape Three Points the abundance of juvenile *Ecklonia* did not differ significantly at each sample from May 1997 to September 1998 (P>.05) (Figure 30b).

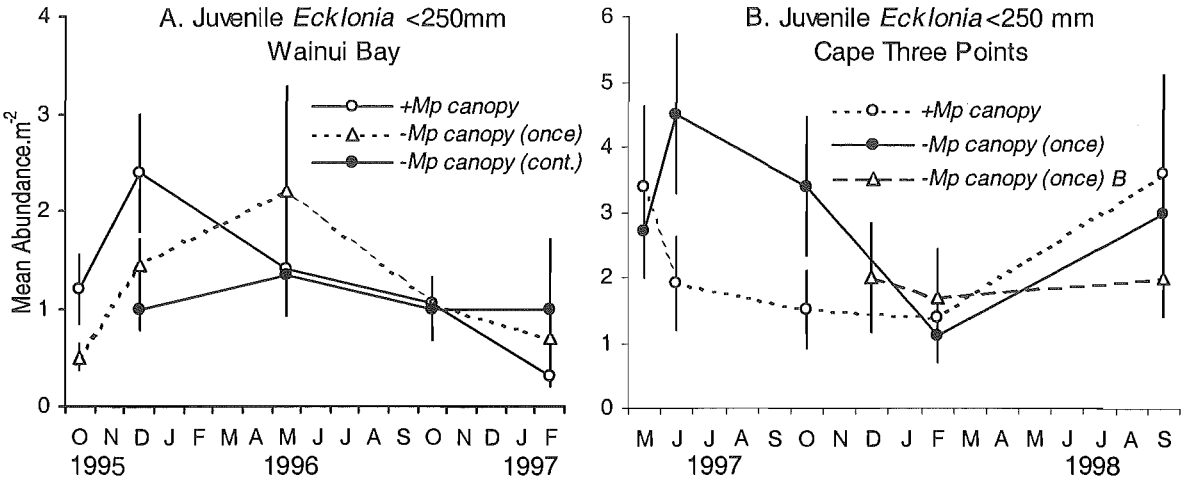

Figure 30 A-B. Mean abundance of juvenile *Ecklonia* (<250mm) within treatment areas ± 1SE at Wainui Bay and Cape Three Points. +*M. p* canopy = control, –*M. p* canopy (once) = surface *Macrocystis* canopy removed once, –*M. p* canopy (cont.) = continual canopy removal (Wainui).

3.3.3.4 Mature Ecklonia *Abundance*

There were no significant patterns in the abundance of mature *Ecklonia*, in relation to canopy removal, in Wainui Bay or Ohinepaka Bay. The standing stock of mature *Ecklonia* (>250mm) did not differ between spring 1995 and spring 1998 (P>.05) (Figure 31a). At Cape Three Points, the abundance of mature *Ecklonia* also did not differ significantly between treatments over the course of the experiment (p>.05) (Figure 31b). A similar result was found in Tory Channel in the abundance of juvenile ($F_{(1,36)}$=.49; p=0.488) or mature *Ecklonia* ($F_{(1,36)}$=.01; p=.92).

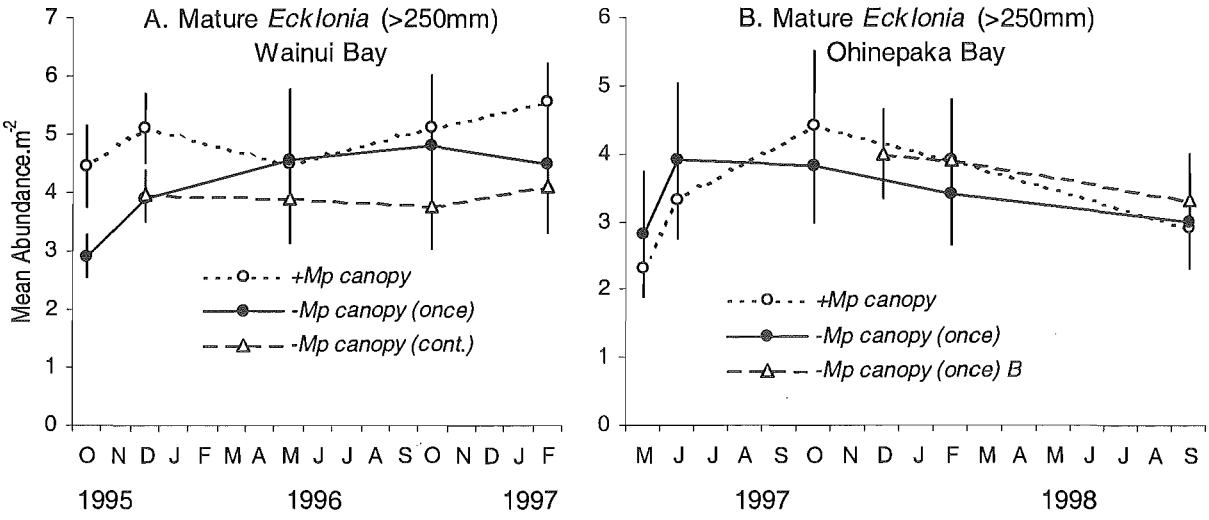

Figure 31 A-B. Mean abundance of mature *E. radiata* (>250mm) within treatment areas ±1SE at Wainui Bay and Cape Three Points. +*M. p* canopy = control, –*M. p* canopy (once) = surface *Macrocystis* canopy removed once, –*M. p* canopy (cont.) = continual canopy removal (Wainui).

3.3.3.5 Mortality

Survival of *E. radiata* was unaffected by removal of the *Macrocystis* canopy at all three sites. In Wainui Bay mortality of tagged plants did not differ between treatments over the period from December 1995 to February 1997 (Figure 32a) ($F_{(2,12)}$=.71; p=.51). Survival at Cape Three Points did not differ significantly between treatments between February 1998 and September 1998 (Figure 32b) ($F_{(2,3)}$=.50; p=.64). Survival of *E. radiata* in Tory Channel was also not significantly affected by canopy removal over the period from March to September 1998 (Figure 32c) ($F_{(1,2)}$=.52; p =.55).

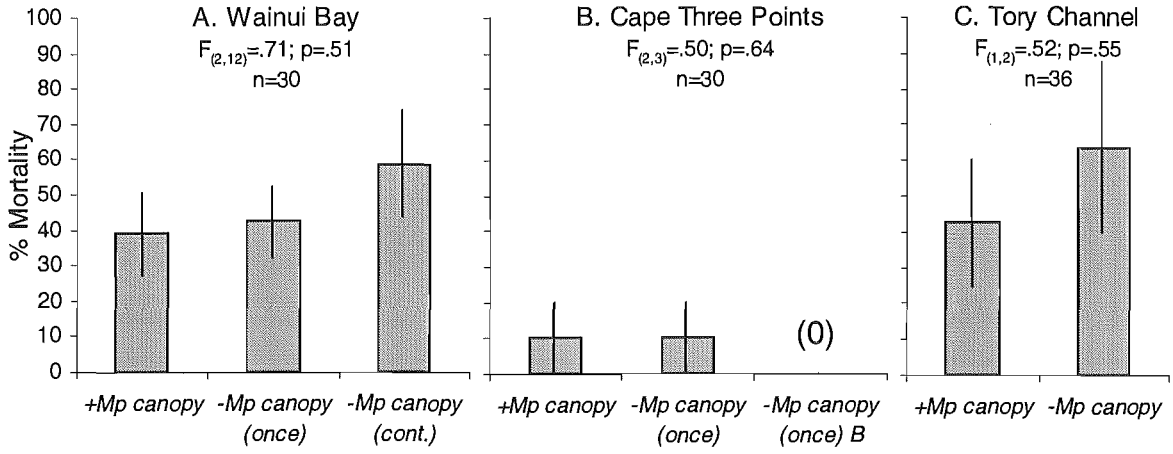

Figure 32 A-C. Percent mortality of tagged *E. radiata* ± 1SE within *Macrocystis* surface canopy removals performed at Wainui Bay (Dec 95 - Feb 97), Cape Three Points (Feb 98 - Sep 98), and Tory Channel (Mar 98 – Sep 98).

3.3.4 Abundance of Other Algae within Series I & II

Series I - Wainui Bay

There was no difference in abundance of juvenile *M. pyrifera* between canopy removal treatments at all sample dates (non sig. at p=.05) (Figure 33a). However, *M. pyrifera* did recruit in large number in all treatments during late spring 1996, this event coincided with a marked decline in surface *Macrocystis* canopy (Figure 24a).

The abundance of >1m *M. pyrifera* was slow to recover following canopy removal (Figure 33b). By summer 1997, the number of *Macrocystis* >1m in removal treatments was only ~25% of original abundance. This, and the steady decline in *Macrocystis* abundance in general, is probably a reflection of the low recruitment observed before spring 1996 (Figure 33a). By spring 1998, the difference between treatments was not significant, but only marginally so ($F_{(3,16)}$=3.22; p=.051), with +*Macrocystis* treatments generally displaying greater abundances of >1m plants. At this time, the mean abundance of >1m plants was 2.88 ± 0.43SE per m^2.

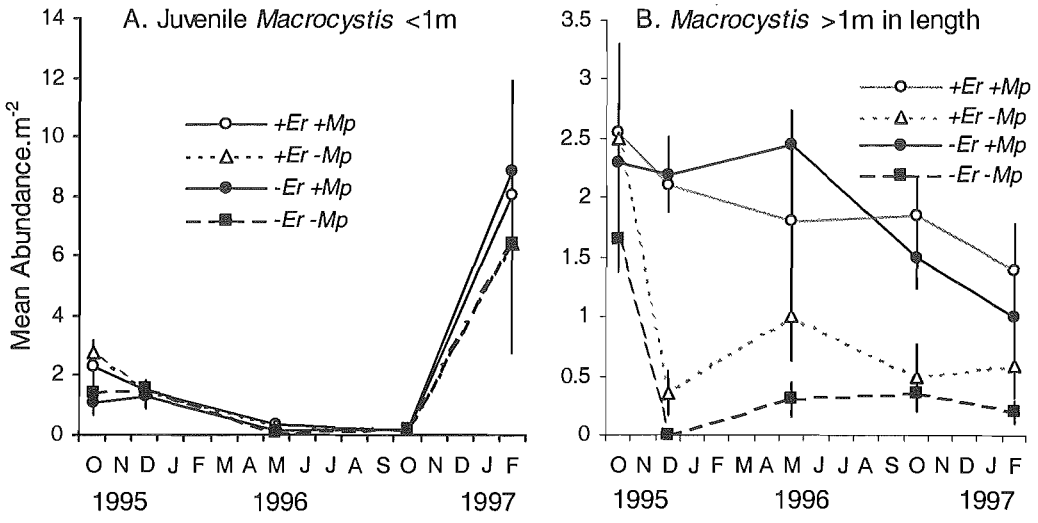

Figure 33 A-B. Mean abundance ± 1SE of (a) juvenile *M. pyrifera* <1m total length and (b) *M. pyrifera* >1m total length within orthogonal once-only canopy removal experiment (series I). +*E. r*/+*M. p* = intact canopy layer, –*E. r*/–*M. p* = canopy layer removed. Spring 1998 not shown.

Carpophyllum maschalocarpum was the only brown alga apart from *Macrocystis* or *Ecklonia* present in any quantity in the deeper regions of the Wainui Bay forest. Small individuals (<100mm) were significantly more abundant within both *Ecklonia* removal treatments prior to canopy manipulation in spring 1995 (Figure 34) ($F_{(1,16)}$=5.54; p=.031) By winter 1996, the abundance of *Carpophyllum* in *–E. r –M. p* had increased to ~2.m^{-2}, and was significantly more abundant than within the control (~0.2.m^{-2}). Subsequently, *Carpophyllum* in the total removal treatment exhibited considerable fluctuations in numbers, declining to ~0.7.m^{-2} by spring 1996 and then increasing significantly within both *Ecklonia* removal treatments over summer 1997 to ~1.5.m^{-2} ($F_{(1,16)}$=10.45; p=.001).

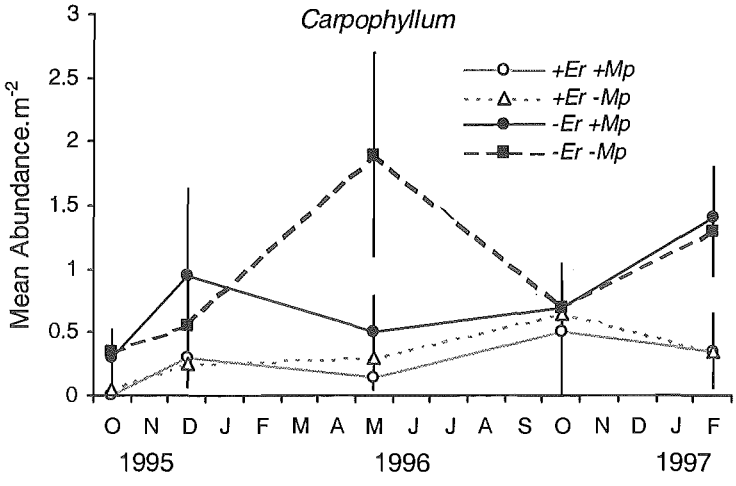

Figure 34. Mean abundance ±1SE of *Carpophyllum maschalocarpum* within orthogonal once-only canopy removal experiment (series I) +*E. r*/+*M. p* = intact canopy layer, –*E. r*/–*M. p* = canopy layer removed.

3.3.4.1 Cape Three Points

Juvenile *M. pyrifera* appeared in the *M. pyrifera* canopy clearance in Cape Three Points during summer 1998 (Figure 35a). At this time, the abundance of juvenile *M. pyrifera* was significantly higher in the first *M. pyrifera* canopy removal (~9.m^{-2}) than in the second *M. pyrifera* canopy removal or the control (~1-2.m^{-2}) ($F_{(2,6)}$=5.22; p=0.048). The abundance of mature *M. pyrifera* never differed significantly between treatments (p<.05) and generally declined in all treatments from winter 1997 to spring 1998 (Figure 35b). The abundance of *Carpophyllum* never differed between treatments at Cape Three Points.

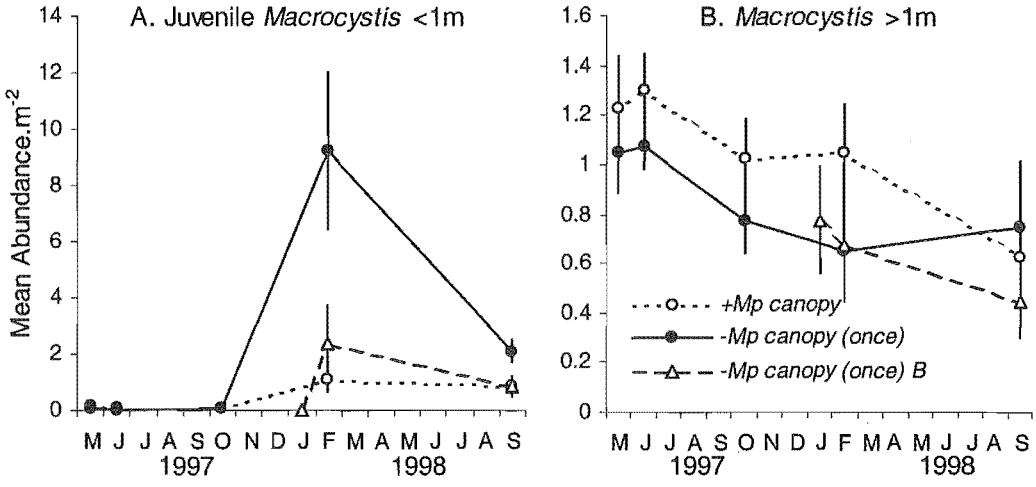

Figure 35 A–B. Mean abundance ± 1SE of juvenile and mature *Macrocystis* within treatment areas at Cape Three Points. +*M. p* canopy = control, –*M. p* canopy (once) = once-only removal of surface *Macrocystis* canopy.

3.3.4.2 Tory Channel

There were considerably more understorey algal species present in the *Macrocystis* forests of Tory Channel than there were in Akaroa Harbour. *Ecklonia* and *Macrocystis* were the only two laminarians present in Tory Channel. The other large macroalgae were all fucalean (5 genera). These were *Carpophyllum sp., Marginariella sp., Xiphophora sp., Sargassum sp.* and *Landsburgia sp.* In addition, numerous red and green (*Caulerpa* sp) algae formed a turf on the substratum. However, there was no discernible effect of *Macrocystis* canopy removal on the abundance of any of the species recorded in quadrats.

3.3.5 Series III - Substrate Clearances

Removal of the overlying kelp canopy and coralline paint produced subtle effects on subsequent occupation of primary free space. Nearly two years after initiation, coralline percent cover was approximately 50% in both treatments where it was removed, well below its initial coverage ($F_{(3,10)}$=12.24; p=0.0002) (Figure 36). The most rapid period of recovery was during the initial 4 months, potentially because areas were reseeded by microscopic fragments of coralline left behind during installation. There was no significant treatment effect of removing overlying canopy, either on the recovery of removed coralline (Table 30), or the persistence of intact coralline (Table 31).

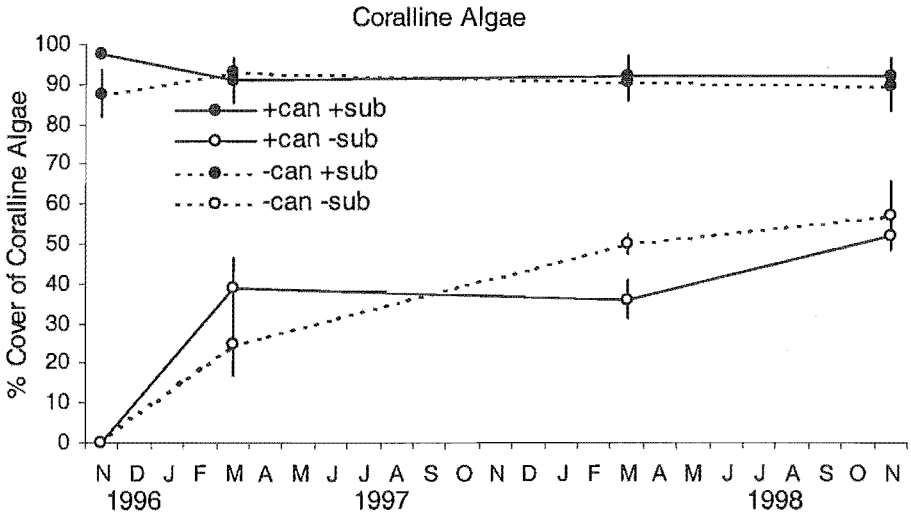

Figure 36. Percent cover of coralline algae within control (+canopy +substrate), substrate-only removal (+canopy –substrate), canopy-only removal (–canopy +substrate), and canopy and substrate removal (-canopy –substrate) treatments (series III) ±1SE.

The abundance of recruits was assessed numerically, and not by percent cover because observed recruits were very small (<5mm) and very sparse. Fucalean algae were never observed in quadrats. Newly recruited laminarians, not identifiable to species because of their small size, were the only algae present in quadrats at the start of the experiment (Figure 37).

By March 1997 there were significantly more laminarian recruits in treatments where the overlying kelp canopies had been removed (Table 32; Figure 37b). In subsequent samples the abundance of laminarians was unrelated to the presence or absence of macroalgal canopy. The removal of coralline algae (substrate clearance) had no significant effect on the abundance of laminarian recruits at any time.

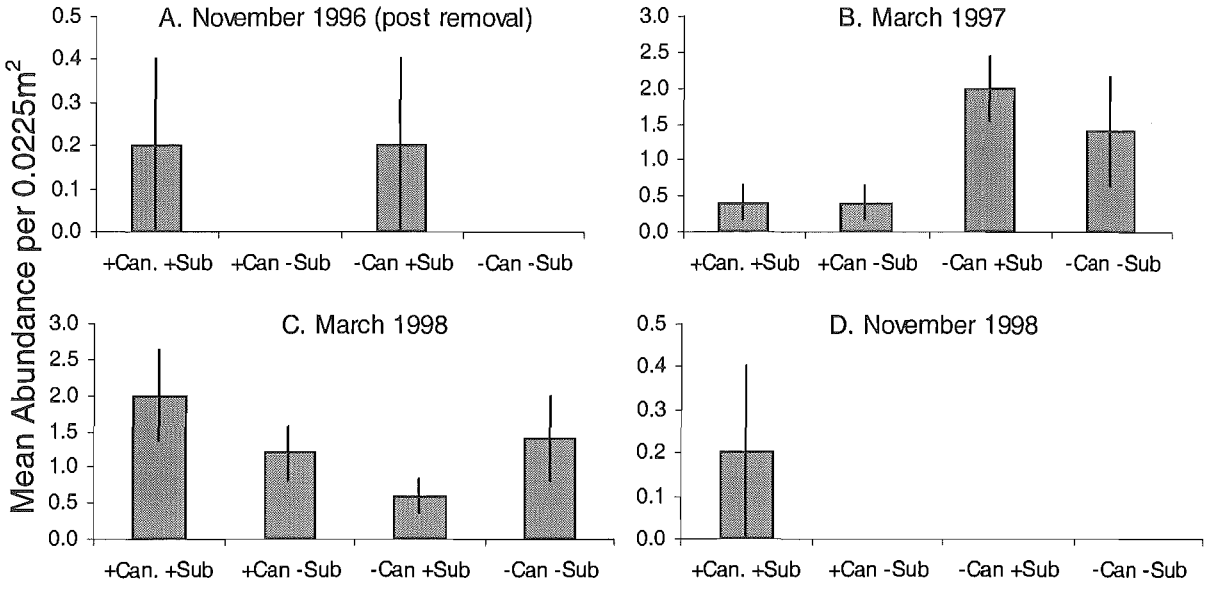

Figure 37. Mean abundance of newly recruited laminarians (*E. radiata* or *M. pyrifera*) within Wainui Bay substrate/canopy removal experiment (series III) ± 1SE.

Species of ephemeral green and red algae also recruited into quadrats, although these never developed beyond small blades 2-3mm in length and were not identified. Green algae first appeared in quadrats in March 1997, at which point their abundance was related to an interaction between the presence of canopy and substrate (Table 34). No green algae appeared when the canopy and substrate were left intact, or when both canopy and substrate were removed. However, when either the canopy or substrate was removed, green algae did recruit. By March 1998, green algae were significantly more abundant in treatments where the overlying canopy had been removed suggesting a long-term effect of canopy removal (Table 35). By November 1998, green algae were only present in one quadrat where both canopy and substrate had been removed. Red algae first appeared in quadrats in March 1997, but only one individual was present at this time (+canopy –substrate). By March 1998, however, there was a significant variation in abundance of red algae due to canopy removal (Table 36). More importantly, there was a significant interaction between canopy removal and substrate removal at this time. This interaction produced the greatest abundance of red algae when both the canopy and substrate were removed, but the lowest abundance when only substrate was removed. Red algae had disappeared from all treatments by November 1998. Sessile and sedentary invertebrates, including limpets, sponges, ascidians, and spirorbid worms showed no distinct distributional pattern across treatments.

Table 30. Percentage cover of coralline in substrate removal treatments (+substrate -substrate)

Source	df	MS	Wilks' λ	F	p-level
Treatment	1, 8	181.6		0.086	0.7767
Time	3, 6		0.0188	104.2	0.0000*
Time x Treatment	3, 6		0.3979	3.026	0.1153

Table 31. Percentage cover of coralline in algal canopy removal treatments (+canopy -canopy)

Source	df	MS	Wilks' λ	F	p-level
Treatment	1, 8	320.1		0.300	0.5987
Time	3, 6		0.8611	0.322	0.8094
Time x Treatment	3, 6		0.3240	4.173	0.0647

Table 32. Abundance of Laminarian recruits – March 1997

Source	df	MS	F	p-level
Canopy	1	2.66	7.04	0.0173 *
Substrate	1	0.30	0.80	0.3832
Canopy x Substrate	1	0.30	0.80	0.3832
Error	16	0.38		

Table 33. Abundance of Laminarian recruits – March 1998

Source	df	MS	F	p-level
Canopy	1	0.60	1.247	0.2806
Substrate	1	0.02	0.003	0.9512
Canopy x Substrate	1	0.43	0.891	0.3592
Error	16	0.48		

Table 34. Abundance of Green algae – March 1997

Source	df	MS	F	p-level
Canopy	1	0.15	0.33	0.5717
Substrate	1	0.15	0.33	0.5717
Canopy x Substrate	1	0.15	8.33	0.0107*
Error	16			

Table 35. Abundance of Green algae – March 1998

Source	df	MS	F	p-level
Canopy	1	1.89	7.24	0.0161*
Substrate	1	0.02	0.09	0.7691
Canopy x Substrate	1	0.02	0.09	0.7691
Error	16	0.261		

Table 36. Abundance of Red algae – March 1998

Source	df	MS	F	p-level
Canopy	1	1.55	10.34	0.0054**
Substrate	1	0.63	4.240	0.0562
Canopy x Substrate	1	2.86	19.12	0.0004**
Error	16			

Table 30 - Table 31. Repeated measures univariate and multivariate analysis of percentage cover of coralline algae within canopy-substrate removal experiment performed in Wainui Bay over four sampling periods.

Table 32 - Table 36. Two-way ANOVAs of abundances of newly recruited macroalgae within canopy/substrate removal experiment. Treatments were: +canopy +substrate (control), +canopy -substrate, -canopy +substrate, -canopy –substrate.

3.3.6 Light

The light environment in the kelp forests of Akaroa Harbour was very poor (Table 37). In areas devoid of both *Macrocystis* and *Ecklonia* canopies, light levels were 50-60% of surface levels at 1m depth and 1-4% at 3m, suggesting that a large proportion of incident light is scattered or absorbed due to the turbidity of the water. Beneath a canopy of *Ecklonia* at 3m depth, light levels were further reduced to <1.0% of surface irradiance.

Table 37. Light levels within the kelp-forests of Wainui and Ohinepaka Bays during one day in May 1997. Numbers represent the average of two sequential readings.

Location	Wainui 11:35am		Ohinepaka 12:40pm	
	$\mu E.m^{-2}.s^{-1}$	% of Surface	$\mu E.m^{-2}.s^{-1}$	% of Surface
Surface	800	-	700	-
1m beneath surface (no canopy)	425	53.1	425	60.7
3m depth (no canopy)	30	3.8	7	1.0
3m depth (beneath *E. radiata* canopy)	8.8	1.1	3.8	0.54

3.3.7 Sediment

The amount of sediment accumulation within sediment traps was generally greater in the absence of a canopy, but was only significantly so over the period from February to March 1998 ($F_{(1,4)} = 11.52$; $p = 0.027$) (Figure 38). This indicates that there may be higher levels of natural sedimentation within areas cleared of canopy, possibly because it settles onto or is disturbed by macroalgae before it can settle.

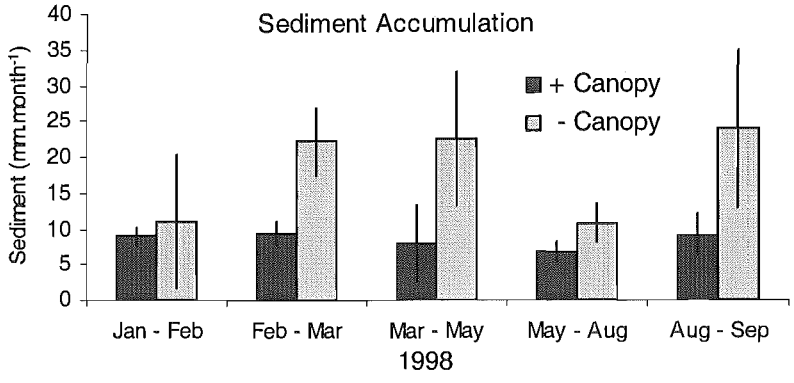

Figure 38. Sediment accumulation within sediment traps placed within the Wainui Bay kelp forest ± 1SE.

3.3.8 Temperature & Rainfall

Mean sea-surface and seafloor (3m depth) temperatures within the kelp forest of Wainui Bay varied between 16°C in summer and 8°C in winter (Figure 39). During spring, summer, and early autumn, sea-surface temperatures were generally warmer than sea-floor temperatures by 0.7°C, suggesting that the water column may be stratified at these times. By late autumn and winter, sea-surface and seafloor temperature correspond more closely,

possibly as a result of increased water mixing during winter storms and the prevalent southerly swell.

Rainfall did not appear to follow any clear seasonal trends (Figure 40). In February 1996 75mm of rain fell in one day (Figure 41). This event corresponded with subsequent high levels of turbidity in inshore areas of Akaroa Harbour, including Wainui Bay (Plate 1)

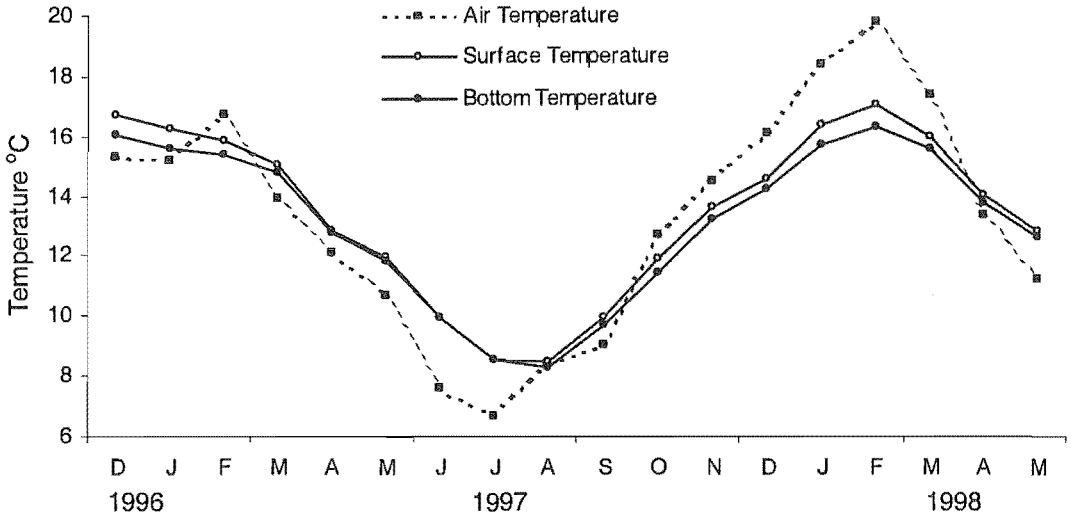

Figure 39. Mean monthly air and sea temperatures. Air temperature data are from Rue Lauvard in Akaroa Township (Source: NIWA). Sea-surface and bottom (depth 3m) temperatures were measured in Wainui Bay.

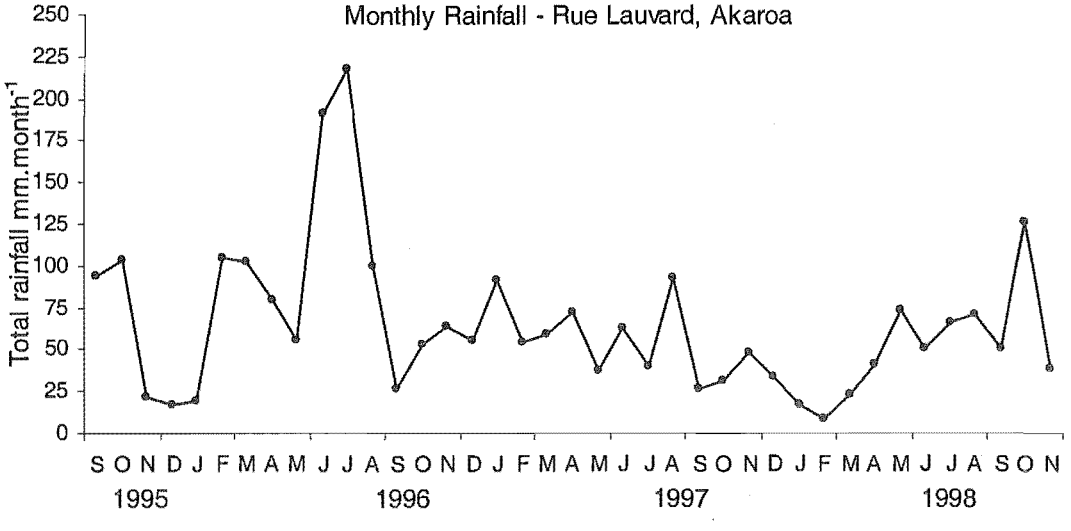

Figure 40. Total monthly rainfall recorded from 1995 to 1998 at Rue Lauvard in Akaroa Township. Source: NIWA.

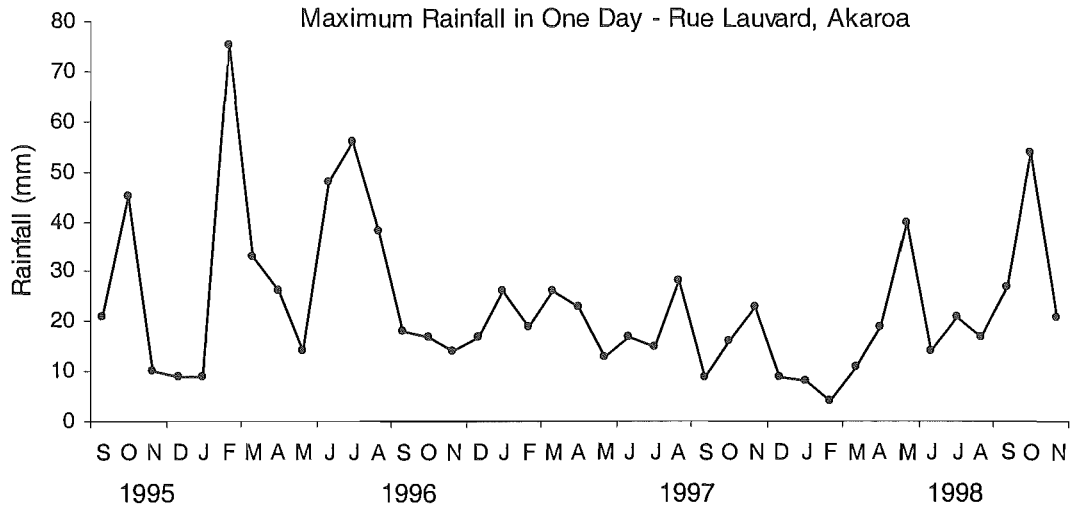

Figure 41. Maximum rainfall in one day for each month from 1995 to 1998. Data were recorded at Rue Lauvard in Akaroa Township. Source: NIWA.

3.4 Discussion

The effects of overlying canopies on understorey species have been examined in numerous studies, both terrestrial and marine (Connell *et al*, 1997; Santelices & Ojeda, 1984; Reed & Foster, 1984; Schroeter *et al*, 1995). In my study, the growth rate of understorey *E. radiata* generally increased following the removal of overlying canopy layers. This was presumably because of increased light; Photosynthetically Active Radiation (PAR) was 2-4 times higher in the absence of an *Ecklonia* understorey (Table 37). Reduction in PAR by the *Macrocystis* canopy was not measured, but its effect on light is probably comparable to that found by other studies. For example, Watanabe *et al* (1992) found that surface canopy removals within the *M. pyrifera* forests of California produced a 4-5 fold increase in PAR in the understorey. Similarly, Pearse & Hines (1979) found that removal of the *M. pyrifera* canopy increased light levels in the understorey from 3 $\mu E.m^{-2}.s^{-1}$ to 65 $\mu E.m^{-2}.s^{-1}$.

Previous studies have attributed increased growth of understorey species following canopy removal to an increase in photosynthesis (Gerard, 1984; Kimura & Foster, 1984; Reed & Foster, 1984; Kennelly, 1989; Kirkman, 1989; Dayton, 1975; Dayton *et al*, 1992; Sjötun *et al*, 1998). Furthermore, Watanabe *et al* (1992) explicitly linked the removal of overlying *Macrocystis* canopies to an increase in photosynthetic by-products (mannitol) in the understorey species *Pterygophora californica*. I did not examine the production of mannitol in *Ecklonia*, but it is likely that higher growth rates were due to an increase in photosynthesis following canopy removal, suggesting light-limitation. Other studies have also demonstrated light-limitation in *E. radiata*. Kirkman (1981) demonstrated that removal of the overlying mature *Ecklonia* canopy in Western Australia resulted in 3 times greater biomass of new recruits after 55 days; plants kept in shaded areas showed little growth. Kirkman (1989) also found that artificial shading of *E. radiata* at 5m depth reduced productivity to levels normally observed at 10m. In northern New Zealand, Novaczek (1984c) found that *E. radiata* at 15m depth grew at half the rate of *E. radiata* at 7m.

A notable feature of my study was that growth was less enhanced (or lamina erosion was faster) when all canopy layers were removed than when just *Ecklonia* or *Macrocystis* were removed (Figure 23). This suggests a trade-off between positive effects of canopy removal (increased light, space), and detrimental effects of canopy removal, where intermediate levels of canopy removal result in greatest growth. The detrimental effects of canopy removal may be related to increased sedimentation observed in complete canopy removal treatments. Akaroa Harbour is characteristically turbid due to long retention times of the

harbour itself and runoff from surrounding hills composed of fine loess (plate 1). Rainfall was especially high around the time when high-levels of lamina erosion were observed during summer – autumn 1996 (Figure 41). In addition, a breakwater adjacent to the Wainui Bay kelp forest was extended during summer 1996. This activity placed a considerable amount of fine sediment into the water, which remained suspended in near shore areas for several weeks before dispersing/settling.

A plausible mechanism for increased sediment deposition following canopy removal is that sediment normally settles onto plants higher in the canopy or is continually swept away by an overlying canopy (Kennelly, 1989). This is supported by the generally higher levels of sediment found within sediment traps in areas devoid of canopies (Figure 38). These high levels of sedimentation may have significantly reduced the growth rate of understorey *Ecklonia* (Figure 23). Lyngby & Mortensen (1995) demonstrated that fine sediment, generated by dredging activity, reduced the growth rate of *Laminaria saccharina* by approximately 20% when it settled on blades, via reduced photosynthetic capacity, and by causing lamina necrosis. In my study, plants covered in sediment were often necrotic and disintegrating at their distal end. Reduced photosynthesis due to sedimentation may allow frond erosion to outpace frond growth, leading to negative growth.

Increased sedimentation is not the only explanation for reduced growth following canopy removal. Previous studies have attributed reduced growth and tissue necrosis in macroalgae to photoinhibition and/or damage by UV light following an increase in light levels (Bruhn & Gerard, 1996; Kubler & Raven, 1994; Wood, 1987). However, photoinhibition and/or UV damage are unlikely to be factors in the reduced growth in my study, even at shallow depths (~3m), due to the turbidity of the water. Furthermore, it is likely that plants would become heavily fouled by epiphytes if light were increased to this degree (Schaffelke *et al*, 1996; Wood, 1987); no such fouling was seen. Another potential explanation is that grazing fish species were attracted to clearings (Jones, 1992; Carr, 1989). However, consumption of algae by resident fish species (e.g. *Notolabrus* spp., *Odax pullus*) was never observed, and algae did not appear to be grazed.

Macroalgal canopies can demonstrably affect the recruitment of algal propagules (Pearse & Hines, 1979; Vadas *et al*, 1992; Kimura & Foster, 1984; Dayton *et al*, 1992). In my study, the recruitment of laminarians <10mm was greatest when overlying macroalgal canopies were removed (Figure 37). However, recruitment was not affected by removal of coralline substrate, which also removed any pre-existing gametophytes and microscopic sporophytes.

This suggests that recruitment was not reliant on the presence of pre-existing propagules. Previous studies are equivocal regarding the importance of dormant stages in the subsequent occupation of canopy gaps. Kimura & Foster (1984) suggested that spores and dormant juveniles of *P. californica* and *M. pyrifera* are probably available throughout the year to enable rapid colonisation following light gap creation. In contrast, Reed *et al* (1997) concluded that the microscopic stages of *P. californica* and *M. pyrifera* had little capacity for dormancy. Additionally, Kirkman (1981) noted that following the removal of the *E. radiata* canopy in Western Australia, no new individuals were seen in cleared areas for 9 months, suggesting that pools of new recruits were generally absent. *Ecklonia* in Akaroa Harbour bear zoosporangial sori throughout the year (Chapter 2, Figure 13), thus gametophytes and microscopic sporophytes may also be present. Conditions beneath the canopies of my study were certainly adequate to support the growth of gametophytes; the minimum light required for *E. radiata* gametophytes to grow and develop normally is ~0.1μE.m^{-2}.s^{-1} (Novaczek, 1984a). My study found instantaneous light levels on the substratum beneath the *E. radiata* canopy to be ~4-8μE.m^{-2}.s^{-1} at midday during May. Mean daily quantum dose is likely to be much lower. Similarly, mean ocean floor temperatures in Wainui Bay never dropped below 8°C, which Novaczek (1984b) found was the minimum temperature required for gametophyte growth in Houghton Bay near Wellington (Figure 39). Furthermore, it is likely that my more southerly populations have lower minimum temperature requirements than northern populations (Novaczek, 1984b). However, conditions may not be adequate to support sporophyte growth (i.e. appearance of recruits) because their development may be limited below ~3.8μE.m^{-2}.s^{-1} (Maegawa *et al*, 1987).

The abundance of laminarian recruits <60mm generally peaked over spring and summer (Figure 21, Figure 28), irrespective of canopy manipulation. Their subsequent survival and growth into juveniles (<250mm) was most suppressed by the *Ecklonia* subcanopy; the greatest numbers of juvenile *E. radiata* were observed in *Ecklonia* canopy removal treatments (Figure 22). Mature *Ecklonia* canopies may actively scour the substratum and potentially remove recently settled propagules (Jenkins *et al*, 1999a; Black, 1974; Velimirov & Griffiths, 1979). Alternatively, recruits that managed to grow over summer may die during winter if light falls below the photosynthetic threshold.

A potentially important determinant of recruitment and growth processes in *E. radiata* is the senescence and recovery of the *Macrocystis* canopy. From 1995 to 1998, the *Macrocystis* canopy displayed a general annual trend of greater biomass in winter than during summer

(Figure 24a). This trend may be a reflection of nutrient limitation in surface waters due to high sea surface temperatures (Figure 39), or the deleterious effects of UV light (Brown *et al*, 1997; North & Zimmerman, 1984; Hay, 1990; Wood, 1987). In contrast to the general depletion of *Macrocystis* canopy in summer, winter storms will tend to result in highly localised canopy loss, although detached plants will often entangle other plants resulting in the creation of still larger canopy gaps. The influence of this pattern will depend on how extensive canopy loss is; removal of whole *Macrocystis* plants significantly affected recruitment and growth in the understorey, however, removal of just the surface *Macrocystis* canopy (to 1m depth) produced virtually no effects on the understorey. This was seen across small and large geographic scales (series II). This suggests that understorey (subsurface) portions of *Macrocystis* are at least as important as the floating surface canopy in suppressing growth and recruitment in the understorey.

A notable feature of my study was that 3 years after both *Macrocystis* and *Ecklonia* canopies were removed from the forest in Wainui Bay, the abundance of large canopy forming *E. radiata* (>500mm total length) within clearances was nearly twice that seen in unmanipulated control areas (Figure 42). There was also a correspondingly lower abundance of *Macrocystis* fronds in these clearances.

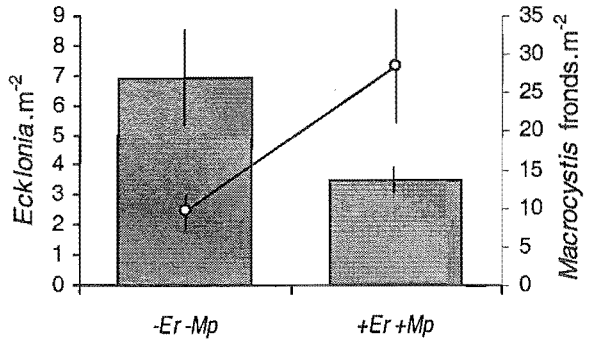

Figure 42. Mean abundance of large (>500mm length) *E. radiata* (bars) and *Macrocystis* fronds (line) in spring 1998, three years after canopy removal in spring 1995 ± 1SE.

This trend suggests that *E. radiata* may be able to physically dominate areas where all canopy layers have previously been removed, if it recruits successfully. The long-term implications of this are important, as *E. radiata* is a long-lived perennial that is more persistent, from year to year, than *Macrocystis*. Coexistence of *Ecklonia* and *Macrocystis* may be possible because disturbance (i.e. canopy-loss) occurs frequently enough to prevent complete suppression of the understorey, yet not so frequently as to preclude subsequent *M. pyrifera* recruitment. This phenomenon may be similar to that found by Reed & Foster

(1984) in Californian kelp forests. There, understorey *Pterygophora* came to physically dominate areas where both *Pterygophora* and *Macrocystis* were removed. Reed & Foster (1984) predicted that if large winter storms ever removed both species, differential mortality of new recruits would eventually result in a dense monospecific stand of *P. californica* that could subsequently suppress recruitment of both species. In my study, *Ecklonia* may persist as a consequence of fluctuations in the *M. pyrifera* surface canopy that are dependent on larger-scale hydrodynamic processes.

Chapter 4: Intraspecific Interactions

4.1 Introduction

Density-dependent patterns of mortality, growth and reproduction have been extensively studied in terrestrial plant populations (Harper, 1977; Watkinson, 1980). Studies of density-dependence in benthic marine algae are less numerous, even though dense aggregation is a common feature of many algal populations (Schiel, 1985; Reed, 1990a). Of studies conducted on marine algae, many have demonstrated reduced growth, survival, and reproduction at higher stand densities in agreement with terrestrial models (Black, 1974; Reed, 1990a; Creed *et al*, 1998; Flores-Moya *et al*, 1996). Negative effects of higher densities are generally attributed to increasing competition for resources such as light, nutrients, and space. However, there is evidence that high density has positive effects in many algal species, especially in relation to growth (Schiel & Choat, 1980; Schiel, 1985; Scrosati, 1996). Increased growth, survival and recruitment at higher densities have been linked to changes in morphology (Andrew & Viejo, 1998), protection from water motion (Schiel & Choat, 1980), suppression of epiphytes (Reed, 1990a), and the creation of a depositional environment in which spores settle more readily (Charters *et al*, 1972). The testing of density-dependent effects in marine algae is hampered by the potentially confounding effects of density-independent factors such as the physical and biological characteristics of microsites (Reed, 1990b; Andrew & Viejo, 1998; Schiel, 1985; Cousens & Hutchings, 1983).

Density dependence is inherently concerned with competition for space and the access to resources that space provides, such as light and nutrients (Watkinson, 1980). However, theoretical modelling of density dependence within plant communities has mainly been in relation to light limitation (Silvertown, 1987; Westoby, 1984). Competition for light in plants is naturally asymmetric, because larger individuals are able to shade smaller individuals. Ultimately, competition for light can lead to the dominance and suppression of smaller individuals by larger individuals (Reed, 1990a; Dean *et al* 1989; Carpenter, 1990). Within a cohort, small initial differences in size can be exaggerated by natural variation of growth rate. Eventually, a size hierarchy may be generated as larger individuals overshadow and suppress the growth of smaller individuals. At high densities, smaller overshadowed plants may fall below the photosynthetic compensation threshold and die. This density-dependent mortality is known as self-thinning. Stands undergoing self-thinning are described in terms of a temporal trajectory on a bilogarithmic plot of stand density (N) versus mean dry-weight (W). In terrestrial studies, an empirical value of -1.5 has been attached to this relationship

(Yoda *et al*, 1963). More recently, an alternate formulation has been widely adopted that plots log *N* against the log of stand-biomass density ($g.m^{-2}$), log *B*. This formulation predicts a slope of -0.5 and overcomes problems of bias associated with mortality of smaller plants (Weller, 1987; Scrosati, 1997). In terrestrial species the value of the self-thinning slope has been demonstrated to be remarkably constant over several orders of magnitude (Westoby, 1984), yet its overall appropriateness to benthic marine algae has remained unclear (Schiel & Choat 1980; Kirkman, 1984; Martínez & Santelices, 1992).

Dominance and suppression precede self-thinning (Weiner & Thomas, 1986; Creed *et al*, 1996), and can be assessed in two ways. The first examines the relative growth rates of plants in relation to their initial size. It is predicted that stands undergoing dominance and suppression exhibit greater relative growth in larger individuals (Westoby, 1984; Reed, 1990a). The second method tracks changes in the size-structure of stands. Algal stands undergoing dominance and suppression will generally exhibit an increase in size-inequality, as a few large plants grow at the expense of others (Arenas & Fernández, 2000; Creed *et al*, 1998; Creed *et al* 1996). High-density stands are expected to display greater inequality than lower density stands.

The processes that occur during dominance and suppression and self-thinning can be combined to make specific predictions about the size-structure of stands as they develop (Weiner & Thomas, 1986). In high-density stands, size-inequality will tend to increase until the onset of self-thinning and then decline as smaller plants die. This approach has previously been used in conjunction with standard log B v log N plots to ascertain the occurrence of self-thinning in several marine algae (Martínez & Santelices, 1992; Arenas & Fernández, 2000; Creed *et al*, 1998).

An additional concept, related yet distinct from self-thinning, is the theory of constant yield, which states that biomass per unit area obtains a fixed value at high densities. This relationship describes a slope of –1 on a bilogarithmic plot of mean biomass (*W*) versus density (*N*); as plant density increases the projected mean plant biomass decreases in proportion. Thus in a series of even-aged stands of different density, mean biomass is expected to be lower in the higher density stands (the Competition-Density effect) (Westoby, 1984). Previous authors have found that mean biomass in mature *E. radiata* is either positively related (Schiel & Choat, 1980), or unrelated (Kirkman, 1984) to stand density. These results suggest that deleterious effects of density may not generally occur in *Ecklonia*. However, there is evidence that populations of *E. radiata* in low light environments

experience intraspecific effects. For example, deepwater *E. radiata* at Goat Island Bay near Auckland generally have a bimodal size distribution (Choat & Schiel, 1982), suggesting a degree of dominance and suppression.

Newly recruited marine algae often form dense aggregations, and density-dependent effects may be more prevalent in these early stages (Black, 1974). This study was prompted by the discovery of aggregations of *E. radiata* juveniles at densities much higher than normally observed. These dense aggregations allowed the testing of several models of density dependent regulation relating to growth and mortality.

4.2 Methods

4.2.1 Juvenile Ecklonia *Stands*

This study centred on unusually dense aggregations of newly recruited and juvenile *Ecklonia* that were discovered within the kelp forest at Ohinepaka Bay. Two stands of juvenile *Ecklonia* were discovered during March 1998 containing 61 plants in total, with a mean length of 27.0mm (±2.6mm SE). In September 1998, seven additional stands were discovered containing 102 juvenile *Ecklonia* in total, with a mean length of 153.0mm (± 8.8mm SE). All nine stands occurred within an area of ~10.m^2 of kelp forest of uniform depth and substrate rugosity. Even though stands were discovered at different times, all stands are assumed to have recruited during spring 1997.

Stand density was estimated by dividing the number of plants within a stand by the area occupied by the stand (max. length x max. width). The effective densities of plants within each stand during September ranged from 166 to 818.m^{-2}. This interpretation of stand density is highly scale dependent, but does provide a means of comparison with other studies. Due to the small numbers of plants involved and the small sizes of stands, edge effects could not be controlled for. However, the aim of this study was to describe the processes occurring within dense stands of juvenile *Ecklonia*, of which edge effects are a natural feature. Plants that lay outside of main clusters were removed so that estimates of density were not biased. Individual plants were mapped relative to permanent features and their total-length measured. The original two stands were sampled again in May, September, and November 1998. The seven additional stands were resampled in November 1998.

Dry-weights of juvenile *E. radiata* were estimated from total length measurements using a relationship determined from previously sampled plants: -

$$\text{Log}_{10}\text{ dry weight (g)} = -0.000014(\text{length})^2 + 0.0138(\text{length}) - 2.4636$$

$$R^2 = 0.98$$

The relationship between total length and biomass was assumed to be constant at different stand densities. Although studies have noted differences in morphology in mature *E. radiata* growing at different densities (Schiel & Choat, 1980), no such effect was noted among the juvenile *E. radiata* of this study.

The degree of size-inequality within stands was quantified using the Gini Coefficient (*G*) from estimates of plant biomass (Bendel *et al*, 1989). *G* has a minimum value of 0 (uniform size-structure), and a maximum value of 1 (greatest inequality of size-structure). The values of *G* obtained in this study were highly correlated with other common descriptors of size

distribution such as skew (r=.68) and the Coefficient of Variation (r=.94). G was chosen as it is regarded as the most robust of available measures (Bendel *et al*, 1989), and also because of its frequent use in other studies of this nature (Creed *et al* 1996; Arenas & Fernández, 2000).

The stands of juvenile *Ecklonia* were examined in relation to several hypotheses outlined in Table 38. These are discussed in more detail in subsequent paragraphs.

Table 38. Summary of the hypotheses tested in relation stands of juvenile *E. radiata*

Theory	Model	Tested by	H_0:	n
Density-dependent growth	Mean growth in high density stands is lower than in low density stands.	ANOVA: Stands nested within density levels.	No difference in growth between stands.	9
Dominance & suppression	Growth of smaller plants is reduced relative to larger plants, and becomes more so at higher density.	Plot of relative growth versus initial size for each stand.	No relationship between relative growth and initial size ($\beta = 0$)	9
	Size inequality will be greater at higher density if competition for resources is asymmetric.	Plot of Gini (G) versus stand density (N) across stands.	No relationship between G and N ($\beta = 0$)	9
Competition-Density Effect	Mean plant biomass is smaller at higher density such that yield ($g.m^{-2}$) remains constant.	Plot log W v log N.	$\beta = 0$	18
Density-dependent mortality	Plants at high density suffer greater mortality.	Correlation between percent survival and density.	$\beta = 0$	9
	Smaller plants within stands suffer greater mortality.	ANOVA: initial size class.	No difference in mortality between size classes	9
Self-thinning	In stands undergoing self-thinning, biomass-density plots follow a trajectory of $-½$.	Plot log B versus log N.	($\beta \neq -½$)	2
	Inequality will decrease as mean biomass increases due to mortality of smaller plants. Empirical model predicts that $G = -0.2(\log W) + 0.7$.	Plot G versus log W.	($\beta \neq -0.2$)	9

4.2.2 Density dependent growth

The general effect of stand-density on growth rate was examined by grouping stands of similar density as replicates (n=3). Stands were readily grouped into low, medium, and high densities with approximate means of $200.m^{-2}$, $400.m^{-2}$ and $>600.m^{-2}$. A nested ANOVA model was used with stands nested in density level. The dependent variable was relative growth rate, calculated as $mm.mm^{-1}.month^{-1}$ over the period from September to November 1998.

4.2.3 Dominance and Suppression

The occurrence of dominance and suppression within stands was assessed through relative growth rates (dynamic) and also by examination of size distributions (static). A significant

positive relationship between relative growth and initial size is suggestive of dominance and suppression of smaller plants by larger plants (Creed *et al*, 1998; Westoby, 1984). Relative growth rate over September to November 1998 was plotted against initial size for each stand.

Evidence for dominance and suppression in static size distributions was examined by plotting Gini (G) against stand-density for each time. An increase in inequality with stand-density is indicative of asymmetric-competition (resource pre-emption), whereas a decline in inequality with density has been interpreted as evidence of two-way competition (resource depletion) (Weiner & Thomas, 1986).

4.2.4 Biomass – Density Relationship

The relationship between biomass and density was examined in relation to the Competition-Density (C-D) effect (Westoby, 1984). Log mean biomass of juvenile *E. radiata* was plotted against log stand density for all stands in September and again in November 1998. The C-D effect predicts that in even aged stands, mean plant biomass will decrease with increasing stand density such that total yield remains constant (the law of constant yield). This produces a slope of –1 on a bilogarithmic plot of mean biomass (W) versus density (N) (Silvertown, 1987). The relationship between W and N was assessed for all nine stands during both September and November (n=18) using Pearson's correlation coefficient; the slope of this relationship (if significant) was obtained by determination of the principal axis (Sokal & Rohlf, 1981). 95% confidence limits about the principal axis were used to test the null hypothesis that $\beta = 0$.

4.2.5 Density Dependent Mortality

Percent mortality within all stands was determined over the period from September to November 1998. The degree of correlation between mortality and initial stand density was tested on arcsine transformed data using Pearson's correlation coefficient. In addition, to test whether initial size had an effect on mortality, juvenile *E. radiata* were divided into three size classes; 0-99mm, 100-199mm, and >200mm. Data could not be normalised, so the analysis was performed as a Kruskal-Wallis ANOVA by ranks. The dependent variable was percent mortality, replicated at the level of stand (n=5; only stands in which plants died were used). The independent variable was initial size class.

4.2.6 Self-thinning

Self-thinning trajectories were assessed in two stands followed from March to November 1998. Stands in the process of self-thinning theoretically follow a trajectory of –0.5 on a bilogarithmic plot of stand biomass density (log B) versus density (log N). To test agreement

with this model, lines were fitted to the bilogarithmic biomass-density plots by determination of principal axes (Sokal and Rohlf, 1981). The degree of association between log *B* and log *N* was analysed using Pearson's correlation. Confidence intervals (95%) of the principal axes were calculated (Sokal & Rohlf, 1981) and used to test agreement with the empirical self-thinning value (β=-0.5).

Gini (*G*) was plotted against mean plant biomass (log *W*) in each stand to determine if there was any evidence of the empirical relationship suggested by Weiner & Thomas (1986). This relationship states that stands follow a trajectory of -0.2 on a plot of *G* v log *W* during self-thinning.

4.3 Results

4.3.1 Density-Dependent Growth

Relative growth ($mm.mm^{-1}.month^{-1}$) was significantly higher in *E. radiata* in medium density stands ($404\text{-}425.m^{-2}$) compared to both the high ($556\text{-}818.m^{-2}$) and low ($166\text{-}227m^{-2}$) over the period from September to November 1998, (Table 39, Figure 43). However, analysis of variance indicated that the allocated density levels only accounted for 20.6% of the total variance in growth. A similar portion of variation was explained by differences between stands within each density level (20.4%). The largest portion (59%) of variation in relative growth remained unexplained in relation to stand density or stand identity.

Table 39. Results of Nested Anova of relative growth rate within stands grouped by density level

Effect	df	SS	MS	F	p
Density-level	2	2.02	1.01	18.54	0.000*
Stand	6	2.00	0.33	6.12	0.000*
Error	106	5.78	0.05		
Total	114	9.80	0.086		

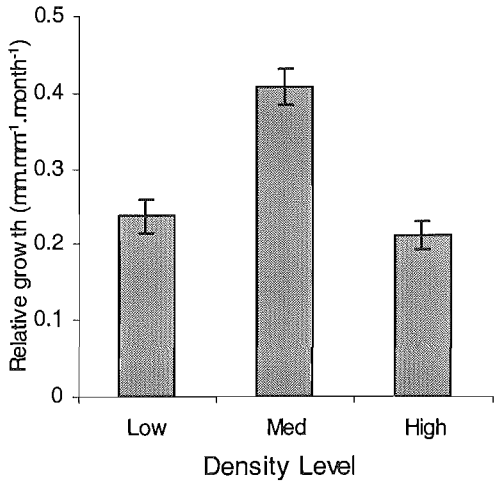

Figure 43. The effects of density on net per capita growth of *E. radiata* over the period from September to November 1998. Data are means (±1SE) of relative growth in total length ($mm.mm^{-1}.month^{-1}$) for 3 stands nested within 3 density levels. Density level 'Low' = $166\text{-}227m^{-2}$, 'Med' = $404\text{-}425m^{-2}$, 'High' = $556\text{-}818m^{-2}$. Means were significantly different by nested ANOVA ($F_{2,106} = 18.54$, P <.001). Relative growth in medium density stands was significantly different from both higher and lower density stands using Tukey's HSD test (P <.05).

4.3.2 Dominance and Suppression

There was a pattern in relative growth in relation to stand density. Relative growth over September to November 1998 was not positively related to initial plant size at low ($166\text{-}227m^{-2}$; r=.05; p=.781; n=29) or medium density ($404\text{-}425m^{-2}$; r=-.33; p=.04; n=39). At high density there was a significant positive relationship between relative growth and initial size ($556\text{-}818m^{-2}$; r=.35; p=.016; n=47). This positive relationship indicates that smaller plants grew proportionately less than larger plants within the same stand. The significant negative

relationship observed at medium density is difficult to reconcile, but may suggest that smaller individuals received protection from larger individuals against some harmful agent, such as water motion or grazing fish.

Gini and stand density did not relate significantly (Figure 44a). The observed lack of a positive relationship suggests that size-hierarchies within stands are unaffected by stand density. However, Gini generally declined in all stands between September and November 1998 (Figure 44a). The absolute change in Gini was significantly correlated with initial stand density (Figure 44b); lower density stands generally experienced a greater decrease in Gini than higher density stands. This result suggests that a positive relationship between stand density and size structure is developing, and may lead to a size-hierarchy at later date.

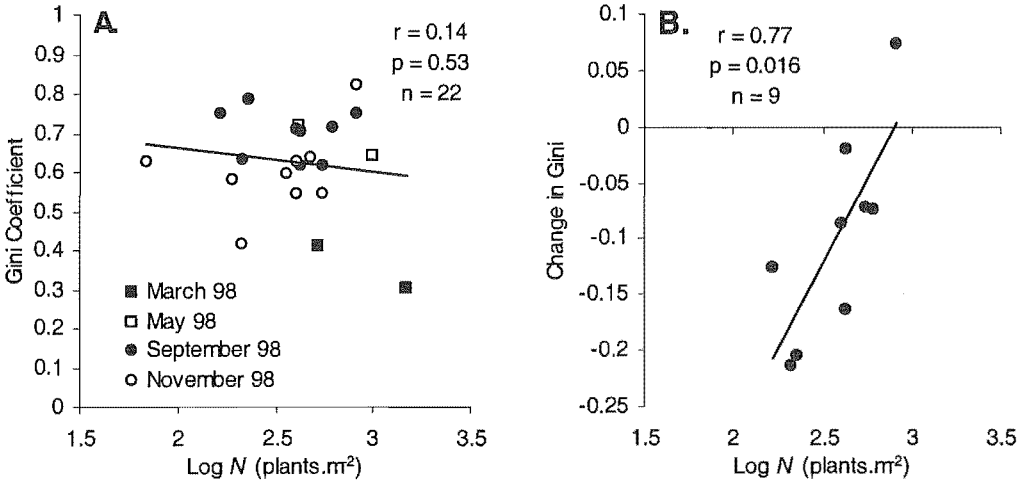

Figure 44 A-B. (a) The relationship between density and the Gini coefficient in stands of juvenile *E. radiata*. *G* was unrelated to stand density across all dates, and also during September 1998 (r =-.15, n = 9, p= .69) and November 1998 (r = .37, n = 9, p = .33). (b) The change in Gini within nine stands of *E. radiata* from September to November 1998 as a function of stand density.

4.3.3 Biomass - Density Relationship

Mean plant biomass (log *W*) was not significantly correlated with density (log *N*) across all stands during both September and November 1998 (r=-.36; p=.13) (Figure 45). Similarly, there is no evidence of constant yield (log *B* v *log N*: r=.29; p=.23). Generally however, stands did not exceed the limit imposed by the –3/2 power law, suggesting that stands may be regulated by this law at combinations of highest biomass and density.

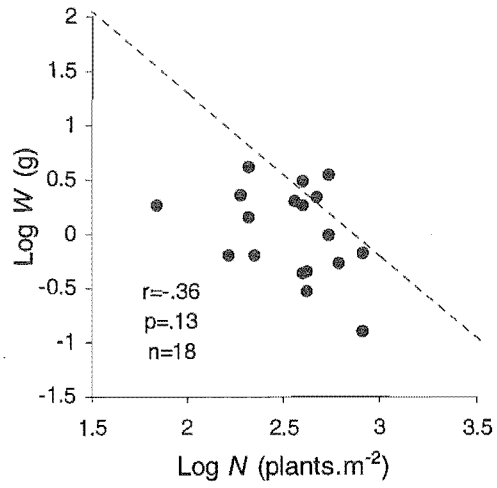

Figure 45. Bilogarithmic plot of stand density against mean plant biomass for all stands of juvenile *E. radiata* during September and November 1998. The principal axis had a slope of -2.72 (95% CI 10.33 to -0.97). The dashed line has a slope of –3/2 and represents the empirical biomass-density boundary.

4.3.4 Mortality

There was no significant correlation between stand density and mortality over the period from September to November 1998 (r=-.43; p=.25, n=9). Mortality was generally low (12.9% ± 6.3% SE), but was highly variable between stands; four stands suffered no mortality at all, while one stand suffered 58% mortality and accounted for 41% of mortality across all stands.

Within stands the survival of juvenile *E. radiata* was significantly affected by initial size (Kruskal-Wallis $H_{2,15}$= 7.637, p=.022). The smallest juveniles (<99mm) suffered significantly higher mortality than plants initially >200mm in length (Figure 46).

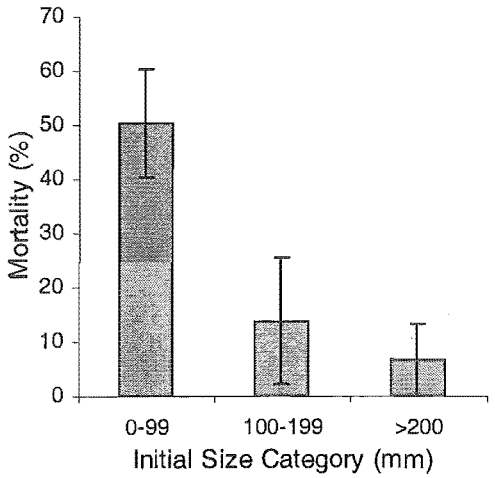

Figure 46. Percent mortality of juvenile *E. radiata* within three initial size categories. Data are mean (± 1 SE) percentage mortality over September to November 1998. Stands that did not undergo mortality were not included in the analysis (n=5). Means were significantly different by Kruskal-wallis ANOVA by ranks ($H_{2,15}$ = 7.637 P = .022),

4.3.5 Self-thinning

Of the two original stands followed from March to November 1998, only one had a trajectory significantly different from zero (β = -4.01), however the 95% confidence limits of this slope suggest that it is also significantly different from –0.5, the slope of the empirical self-thinning line (Figure 47, Table 40).

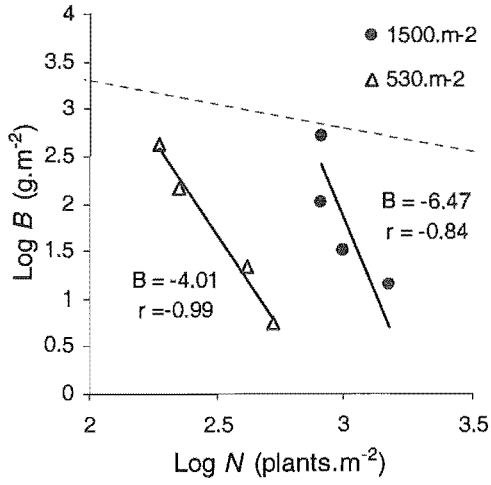

Figure 47. The relationship between stand biomass density (log *B*) and density (log *N*) in two stands followed from March to November 1998. Dashed line represents the empirical self-thinning line (-0.5).

Table 40. Relationship between biomass density (log *B*) and density (log *N*) determined from slope of principal axis.

Log B v log *N*	r	F	p	β	α	95% CI of β		
Initial density 1500.m^{-2}	-0.84	4.99	0.155	-6.47	21.25	7.02	to	-2.08
Initial density 530.m^{-2}	-0.99	142.25	0.007*	-4.01	11.71	-6.21	to	-2.93

4.3.6 Gini & Biomass

One noteworthy relationship did support the occurence of self-thinning processes in juvenile stands. The relationship between inequality and biomass followed the curved trajectory predicted by Weiner & Thomas (1986) (Figure 48). *G* generally increased with increasing mean biomass up to a maximum of 0.1g dry-weight through March and May, and then declined through September and November. In the November sample *G* was significantly negatively correlated with mean biomass across stands (r =-.96, n=9, p<.01). However, the slope of the principal axis (-.45) was significantly steeper than the predicted empirical relationship (-0.2) (Weiner & Thomas, 1986). The 95 % CI of the slope were from -.34 to -.58.

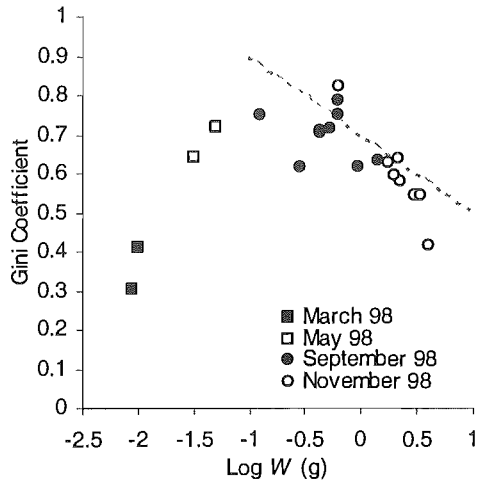

Figure 48. The relationship between mean plant biomass and the Gini coefficient across all survey dates. *G* and log *W* were unrelated during September 1998 (r = -.35, n = 9, p = .357). By November 1998 G and log *W* were significantly correlated (r = -.96, n = 9, p < .000). The dashed line represents the empirical relationship proposed by Weiner & Thomas (1986) (y = -0.2x + 0.7).

4.4 Discussion

The stands of juvenile *E. radiata* examined in this study showed mixed concordance with the models of density-dependent regulation outlined in Table 38. There is evidence of density dependent growth among juvenile *E. radiata*. In my study, relative growth rate was highest at intermediate density levels (Figure 43), and may represent a balance between positive and negative density effects.

The positive relationship between growth and density is concordant with the results of Schiel (1985), who found increased growth in the fucoids *Sargassum sinclairii* and *Carpophyllum maschalocarpum* at higher densities. Andrew & Viejo (1998) similarly found that *Sargassum muticum* grew longer at higher densities. Schiel (1985) suggested that growth might increase with density if competition for light or nutrients were low, or if higher density afforded protection from adverse water motion. At the other extreme, a negative relationship between growth and density is also concordant with numerous terrestrial (Harper, 1977), and marine studies (Black, 1974; Creed *et al* 1996). Creed *et al* (1998) demonstrated that *Laminaria digitata* and *Fucus serratus* plants grew slower at higher densities. Reed (1990a) artificially thinned natural populations of *Pterygophora californica* to four different densities and found that individuals at lower densities experienced increased growth. Black (1974) similarly found higher growth among stands of *Egregia laevigata* thinned to one-third natural density.

Reduced growth at high density is generally attributed to competition for nutrients (symmetric) or light (asymmetric) (Creed *et al*, 1998). I found no initial evidence of asymmetric competition in my stands; larger plants did not appear to grow at the expense of smaller plants across all densities, and there was no evidence of greater inequality in size structure at higher densities (Figure 44a). However, there was a trend for low density stands to become 'more equal' than high density stands over the period from September to November (Figure 44b). This may presage the development of a size hierarchy in high density stands. Kenkel (1988) suggested that the type of competition (symmetric or asymmetric) that plants undergo will depend on their stage of development. Early stages are unlikely to shade each other, but will compete proportionally for nutrients if these are limiting. Additionally, Reed (1990a) suggested that asymmetric competition in high-density stands of macroalgae is related to depth and species architecture, both of which affect the ability of plants to intercept light. In my study, juvenile *E. radiata* were generally close enough to physically interact (Figure 49), yet at their present stage of development, their

growth form probably precludes the formation of a persistent canopy that can actively shade other plants. Nonetheless, these results suggest that a dominance hierarchy may eventually develop as high density stands mature (Figure 44b).

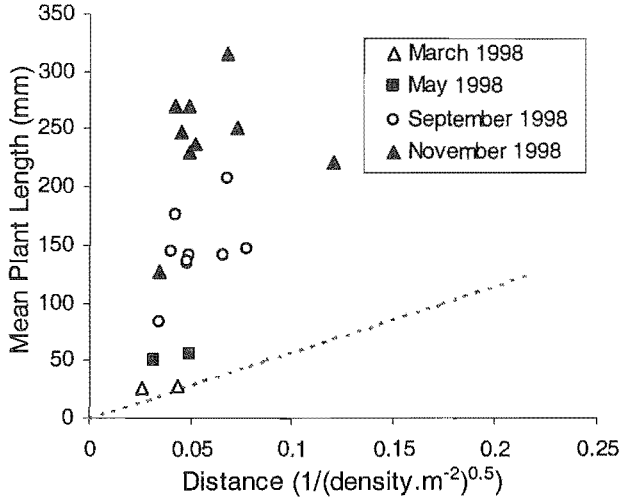

Figure 49. The relationship between mean plant length and stand density (expressed in terms of distance to nearest neighbour) through time. Below the dashed line plants are unlikely to interact physically because they are either too small or too far apart.

Although stand density does appear to play a significant role in determining growth rate, of equal importance was variation between individual stands. This may reflect the influence of wider patterns of hydrology, irradiance, canopy cover, and other biotic and abiotic factors on the growth of juvenile *E. radiata* (Chapman, 1973; Reed, 1990b). The stands of juvenile *E. radiata* in my study were situated beneath a surface-canopy of *Macrocystis pyrifera* that experienced large fluctuations in density and extent on both large and small temporal and spatial scales. These fluctuations are likely to result in variation in the understorey light environment over similar spatial and temporal scales (Wing *et al*, 1993; Gerard 1984). In Chapter 3 I demonstrated that juvenile *E. radiata* are responsive to manipulations in surface canopy. Variability in growth due to differences in microhabitat may be an important determinant of the relative performance of juveniles in different stands (Reed, 1990a; Schiel & Foster, 1986; Vadas *et al* 1992). Similarly, various factors may favour the dense recruitment of algae but not their subsequent growth to maturity, or vice versa (Creed *et al*, 1998; Foster, 1975b). Successful recruitment of benthic algae is often the result of chance events. Vadas *et al* (1992) found that the survival of early post settlement stages was dependent on up to six intrinsic and 17 extrinsic factors. Of these, the effects of grazing, overlying canopies and turfs were generally the most important. Similarly, Kirkman (1981)

found that recruitment of *E. radiata* in Western Australia was patchy in nature, and related more to site availability than seasonal availability of propagules.

The absence of a significant relationship between mean biomass and density suggests that yield was not constant across stands, but instead varied independently of density (Figure 45). This result is similar to that found by Kirkman (1984) for a mature population of *E. radiata* in Western Australia. There, the variation in density explained by plant weight varied monthly, and yield was not constant at densities up to ~60.m^{-2}. Schiel & Choat (1980) also found non-constant yield in mature *E. radiata* from northern New Zealand at densities up to ~45.m^{-2}, although their relationship between mean biomass and density was positive. In my study, the lack of a relationship suggests that resources were not limiting even at the highest densities observed, and stands had not achieved the greatest 'packing' of biomass within a given area.

There was no evidence of density dependent mortality in any stand of juvenile *Ecklonia*. Mortality within stands was related to density-independent factors, such as initial size (Figure 46), and stochastic events, which caused the loss of 58% of individuals within one stand. A consequence of the low overall mortality is that empirical self-thinning does not appear to be present in these stands of juvenile *Ecklonia*. The thinning trajectories followed by stands from March to November 1998 were considerably steeper than the predicted empirical relationship of log B = -0.5log N (Figure 47). Such steep trajectories may be a reflection of biomass accumulation before the onset of self-thinning (Westoby, 1984). However, the point at which self-thinning begins is ill-defined, and has been vaguely linked to a mortality rate greater than 20% (Westoby, 1984; Weller, 1987). By this criterion, self-thinning would have occurred in at least one stand, but it is difficult to reconcile the observed trajectory (-4.0) with empirical theory. Watkinson (1980) suggested a range for self-thinning slopes of between -1.3 & -1.8 (log W v log N), and regarded this as invariable. However, recent evidence suggests that no fixed slope value exists, but each species/stand generates its own value dependent on numerous species-specific and environmental parameters (Scrosati, 1997). Weller (1987) demonstrated that -0.5 is just one of several possible values and stated that importance should instead be given to the ecological interpretation of differences among slopes. Similarly, self-thinning slopes based on terrestrial studies may not adequately reflect the innate differences between marine algae and land-based plants, such as nutrient uptake and support structures (Schiel & Choat, 1980; Westoby, 1984).

Although stands did not follow the empirical model proposed by Yoda *et al.* (1963), they did display a pattern consistent with the self-thinning model of Weiner & Thomas (1986). Inequality generally increased in stands from March to September. By this time stands had approached the threshold of the proposed empirical relationship. Thereafter, from September to November, inequality generally decreased in response to the greater proportional mortality of smaller individuals. This pattern suggests that shading may be important in structuring stands of juvenile *E. radiata* (Weiner & Thomas, 1986).

Mature *E. radiata* in the kelp forests of Akaroa Harbour generally occur at low densities of ~4.m^{-2}, although they often form loose aggregations because recruitment is favoured within the holdfasts of established plants (Anderson *et al*, 1997). The occurrence of several high-density clumps of even-aged juvenile *E. radiata* in a relatively small area was therefore an unusual phenomenon. The conditions that lead to such highly localised episodes of recruitment remain unclear, but may be related to fluctuations in grazer abundance, sedimentation, or surface canopies. Unfortunately, manipulative experiments that addressed questions of density dependence by artificially aggregating sparse juveniles failed, because plants suffered lamina necrosis, epiphyte growth, and callous formation on the stipe.

The models tested in these stands were developed to explain intraspecific interactions in terrestrial plants. While my data exhibit general agreement with some of these models, density dependence does not appear to have a governing influence on the initial structuring of these juvenile stands. However, it is unlikely that observed rates of biomass accumulation could be sustained for much longer without considerable density-dependent effects (Schiel, 1985). The relationship between Gini and biomass through time suggests that density dependent patterns may develop as juvenile stands grow. These patterns may through time lead to the observed low densities of mature *E. radiata.*

Chapter 5: Algal – Herbivore Interactions

5.1 Introduction

There is an abundant literature on the effects of grazing invertebrates in both intertidal and subtidal benthic communities (Andrew, 1994; Dean *et al*, 1989; Lubchenco, 1982; Jenkins *et al*, 1999b). However, the role played by grazing invertebrates in marine systems remains relatively controversial (Estes & Harrold, 1987; Elner & Vadas, 1990). That grazing invertebrates can have an important influence on the distribution and abundance of algae is not disputed (Black, 1976; Breen & Mann; 1976a, 1976b; Harrold & Reed 1985; Leonard, 1994). What is not clear is the importance of grazing in relation to other biotic and abiotic processes that structure kelp communities (Schiel & Foster, 1986; Foster & Schiel, 1987; Ayling, 1981).

Variation in grazer abundance has been related to recruitment processes (Choat & Schiel, 1982), disturbance (Cowen *et al,* 1982), starvation (Harrold & Reed, 1985; Dean *et al*, 1984), competition (Tegner & Dayton, 1991), disease (Hagen, 1995; Pearse & Hines, 1979), topology (Andrew, 1993), and the disappearance of predators (Estes *et al,* 1978). Regardless of specific causes, fluctuations in grazer abundance can have important consequences on community structure, as grazing is an important form of biological disturbance in communities where space is limiting (Ayling, 1981).

The rocky subtidal around New Zealand contains a rich assemblage of grazing invertebrates, some of the most conspicuous of which are molluscs (Choat & Schiel, 1982). Previous studies suggest that the assemblage of grazing molluscs in New Zealand plays an important role in structuring algal communities (Trowbridge, 1995; Schiel 1981; Choat & Andrew 1986; Choat & Schiel, 1982; Ayling, 1981). In northern New Zealand, urchin grazing maintains encrusting communities by preventing the development of turf (Ayling, 1981). Consequently, algal spores and diatoms become more accessible to herbivorous gastropods that are themselves unable to maintain the encrusting community. The abundance of herbivorous gastropods is therefore positively correlated with the abundance of urchins and the persistence of encrusting communities.

Macroalgal canopies are of great importance to the macroinvertebrates that live on or beneath them, and feed either directly or indirectly on algal productivity (Mann 1973; Bustamante *et al*, 1995). However, processes that affect invertebrate abundance within kelp forests are only beginning to be understood (Duggins *et al*, 1990, Schroeter *et al*, 1996; Taylor, 1998, Taylor & Cole, 1994).

The laminarian canopies in Akaroa Harbour are substantial, and form an extensive and productive habitat for numerous herbivorous molluscs. Species include trochids (*Trochus viridus, Cantharidus purpurea*), limpets (*Cellana* spp.), abalone (*Haliotis iris*), and cats-eyes (*Turbo smaragdus*). Particularly large specimens (up to 90mm Ø) of the turbinid gastropod *Cookia sulcata* are also very abundant. The omnivorous seastar (*Patiriella regularis*) is also present in large numbers. However, urchins (*Evechinus*) are notable for their low abundance. The substratum in the kelp-forests of Akaroa Harbour is characterised by near complete cover of encrusting coralline algae (*Litholamnion* spp.), interspersed with sessile invertebrates such as sponges and spirorbid worms. Articulated corallines, turfs and fleshy red algae are generally absent beneath the laminarian canopy in these localities (plate 2).

This chapter consists of four sections. The first provides a general description of macroinvertebrate abundance at Wainui Bay, Ohinepaka Bay, Cape Three Points, and Tory Channel (Figure 2). The second is an investigation into the effect of algal canopies on grazer abundance. Here, I examined the hypothesis that the dependence of grazing invertebrates on algal canopies may be reflected through local changes in abundance following canopy removal. Potential mechanisms for this include behavioural responses to loss of habitat, or the enhancement of diatoms and algal propagules on which grazers feed. Thirdly, I examined the effect of grazers on algal recruitment in a small-scale exclusion experiment. Finally, the effect of a very large and very abundant herbivorous grazer (*Cookia sulcata*) on macroalgal recruitment is examined in a large scale inclusion exclusion/experiment. I hypothesised that *Cookia* may play an important role in structuring these forests by consuming algal spores and recruits.

5.2 Methods

5.2.1 Invertebrate Sampling

The abundance of large macroinvertebrates was assessed in Ohinepaka and Wainui Bays on eight occasions from winter 1995 to spring 1998 and at Tory Channel in autumn 1996. $1m^2$ quadrats (n=10) were placed on the substratum at random intervals along two randomly placed 20m transects. All large invertebrates were identified and counted within quadrats. I was not interested in seasonal variations in abundance, so samples from all times were pooled. Macroinvertebrates were also assessed at Cape Three Points. $1m^2$ quadrats (n=5) were sampled within each of the control treatments of the canopy removal experiments performed at this site (Chapter 3, Series II). All large invertebrates were identified and counted within quadrats. Sites were compared by one-way anova, post-hoc tests on significant results were by Tukey's HSD test ($p<.05$).

5.2.2 Canopy-Invertebrate Interactions

The response of macroinvertebrates to canopy removal was examined within the canopy clearance experiment detailed in Chapter 3 (Series I). Within each 2 x 2m clearance, all macroinvertebrates were identified and counted. To determine if there were any immediate effects of canopy removal, the abundance of each invertebrate was analysed using data from December 1995, 2 months after canopy removal, as a two-factor ANOVA. Fixed factors were the presence or absence of *Ecklonia* and the presence or absence of *Macrocystis*.

5.2.3 Exclusion of Grazers from Primary Substrate

Previous experiments yielded results that indicated a poor occupancy of primary substrate by macroalgae (Chapter 3, Series III). It was hypothesised that grazing invertebrates may consume algae before they become visible as recruits. An experiment was set up to examine the effect of grazers on primary substrate utilisation. Cages were used to exclude grazers from primary substrate.

Concrete slabs measuring 190mm x 190mm x 40mm were used as a proxy for primary substrate. The benefits of using slabs was that they were uniform in size and surface rugosity, and it was not necessary to remove an existing coralline layer, fragments of which can remain and re-seed. In preparation, the slabs were placed into a slow-flowing freshwater stream for approximately 2 months, to leach residual lime from the cement.

The experimental design consisted of three treatments (n=5); uncaged, caged (exclusion), and cage control. Cages were constructed from 20mm Netlon™ mesh and designed to fit

over the concrete slabs leaving a gap of ~100mm between the cage roof and the top of the slab. Cage controls were similar to cages, but only had roofs with no sides. Slabs/cages were deployed during Winter 1997 onto the substratum within the kelp forest at Wainui Bay, and sampled in situ for macroalgal recruits at every opportunity until spring 1998. Sediment accrual, which was cleared from treatments at every inspection, was not quantified.

5.2.4 *Exclusion/Inclusion of* Cookia sulcata

The effect of *Cookia sulcata* on the recruitment and subsequent growth of macroalgae was assessed using inclusion/exclusion cages. Large frames (750 x 750 x 200mm) consisting of tubular PVC piping were covered with 20mm Netlon™ mesh (Figure 50), and attached to the substratum using Ramset™ "hit and twist" masonry anchors. A 200mm wide Netlon™ skirting was attached around the base of each cage, and weighed down with rocks to provide further stability and to prevent movement of *Cookia* beneath cage walls. The tops of cages were left open; fully enclosed cages would reduce light, become fouled by drift algae and epiphytes and increase the drag on cages considerably. Also, the effects of grazing fish species (*Notolabrus* spp., *Parika*, *Odax*, *Forsterygion* spp.) were not being specifically examined, and to exclude them would confound the effect of *Cookia* and require the use of multiple controls. To prevent *Cookia* from entering or leaving cages, a series of 'ramparts' made of Netlon™ mesh were placed around the top perimeter of cages. The edges of the Netlon™ were cut to leave 20mm spikes and were configured to permit easy travel in one direction only; i.e. in or out (Figure 50 inset). There was no way of preventing accidental "fallout" of *Cookia* from adjacent macrophytes into cages, but this event was deemed rare enough to be disregarded. The 20mm mesh allowed smaller motile organisms such as starfish, trochids and triple-fins to pass, relatively unhindered. Larger organisms, such as *Haliotis* and *Turbo*, were either too rare or immobile to warrant special consideration in this regard.

The experimental design consisted of three treatments; *Cookia* inclusion, *Cookia* exclusion, and a control consisting of a frame with no mesh (this controlled for disturbance during installation of the cages, in addition to functioning as a control treatment). *Cookia* inclusion involved placing 5 large *Cookia* (Ø ~80mm) within the cages at a density of ~9.m^{-2}, 4-5 times higher than natural density. Such high densities were used because the cages were not completely *Cookia*-proof, and it was anticipated that losses would occur. In addition, observations indicated that *Cookia* were often naturally aggregated in small patches. To reduce the possibility of *Cookia* entering cages, all *Cookia* within a ~2m radius

of exclusion cages were removed (or used within inclusion treatments). Treatments (n=3) were placed randomly within the forest at Ohinepaka Bay, but were stratified to the extent that cages required flat areas of reef relatively free from macrophytes. Abundances of macrophytes, motile and sedentary invertebrates and percent cover of sediment were assessed initially and at approximately 4-month intervals for one year. Percent cover of sediment was assessed using a square of Netlon™ mesh 250 x 250mm in area having 20 randomly chosen marked intersections. The mesh allowed percent cover to be assessed by counting where sediment coincided with marked intersections without disturbance of the sediment. At every survey, and whenever possible in between, *Cookia* numbers were checked within treatments and appropriate corrections made.

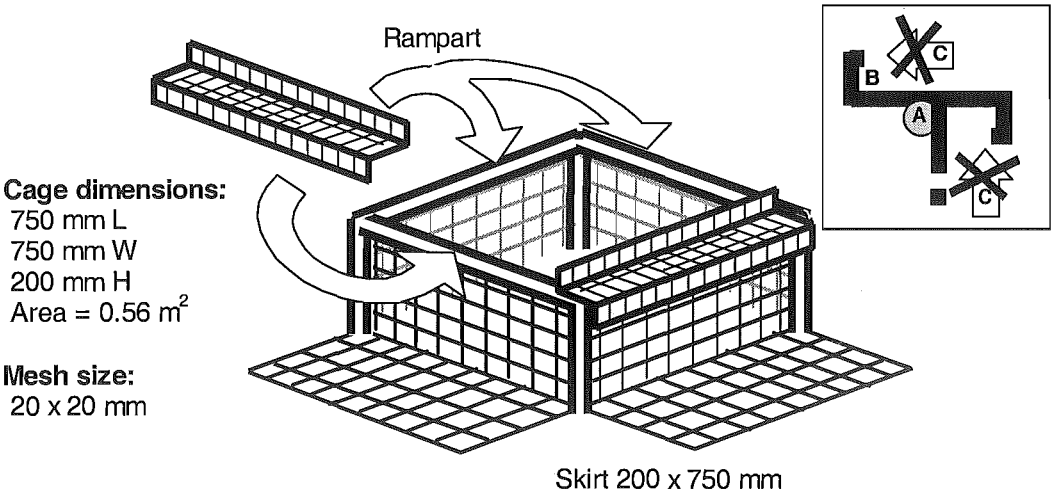

Figure 50. Design of *Cookia* inclusion/exclusion cages, consisting of PVC tubing frame, covered with Netlon mesh. Ramparts and skirting were added to improve retention/exclusion. Inset: side view of rampart showing how movement of *Cookia* was restricted. A= PVC tube B=Rampart C= Path of *Cookia*.

Prior to analysis, percent cover was arcsine transformed and count data square-root transformed if required to correct non-normal data. Data were analysed as a two-way anova. The first independent variable (fixed) was treatment (inclusion, exclusion, control), the second was time, which was treated as random. Probabilities were considered significant at $P<.05$.

5.3 Results

5.3.1 Invertebrate Sampling

Large invertebrates were generally more abundant at the three Akaroa Harbour sites than at Tory Channel (Figure 51). *Cookia*, *Turbo*, *Trochus*, *Cantharidus* and *Cellana* were never encountered within quadrats at the Tory site. *Haliotis* were significantly more abundant at Wainui Bay site (~1.m^{-2}) than any of the three other sites ($F_{(3,236)}$=12.91; p<.01). *Cookia* had an abundance of ~2.m^{-2} at Ohinepaka Bay and were significantly more abundant than at either Wainui Bay or Cape Three Points ($F_{(2,227)}$=19.11; p<.01). *Evechinus* abundance did not differ significantly between Cape Three Points and Tory Channel ($F_{(1,78)}$=.02; p=.88). *Evechinus* were present at Wainui and Ohinepaka Bays, but were never encountered in quadrats. *Turbo* were significantly more abundant at Wainui Bay than at Cape Three Points ($F_{(2,227)}$=9.19; p<.01), Ohinepaka Bay had intermediate numbers of *Turbo*. The trochids *Trochus* and *Cantharidus* were the most abundant herbivorous gastropods present in Akaroa Harbour and did not differ significantly between sites ($F_{(2,207)}$=1.43; p=.24). *Cellana* were significantly more abundant in Wainui Bay than in either Ohinepaka Bay or Tory Channel ($F_{(2,197)}$=7.86; p<.01). The seastar, *Patiriella,* had similar levels of abundance at all three Akaroa sites (~2.5.m^{-2}), but were significantly less abundant at Tory Channel ($F_{(3,236)}$=6.97; p<.01).

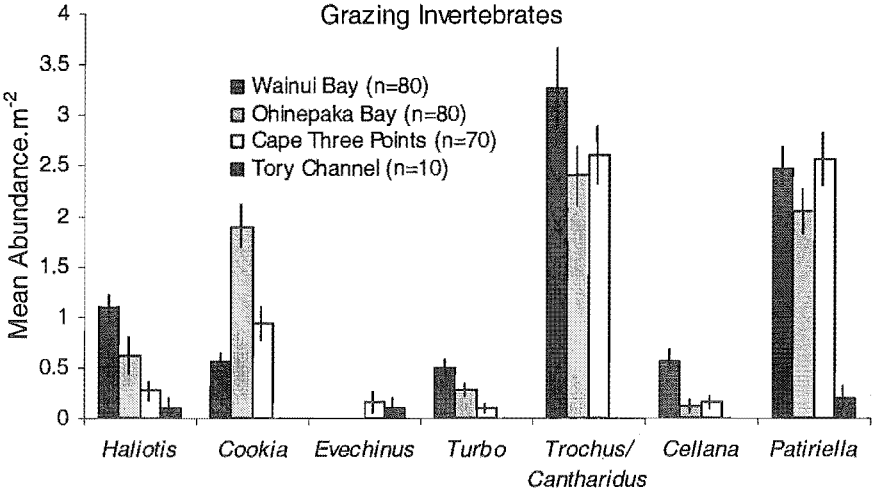

Figure 51. Mean abundance of large macroinvertebrates at four sites ± 1SE. Data were obtained from randomly placed 1m^2 quadrats.

5.3.2 Canopy-Invertebrate Interactions

The response of large macroinvertebrates in Wainui Bay to canopy removal was species specific; *Cookia sulcata* displayed no significant response (Figure 52a, Table 41), while *Haliotis* and *Turbo* both showed significant responses only to the removal of *Macrocystis* (Table 42, Table 43). The responses of these two species were contrasting; *Haliotis* was lower in abundance where *Macrocystis* was removed, while *Turbo* was lower where *Macrocystis* was left intact (Figure 52b-c).

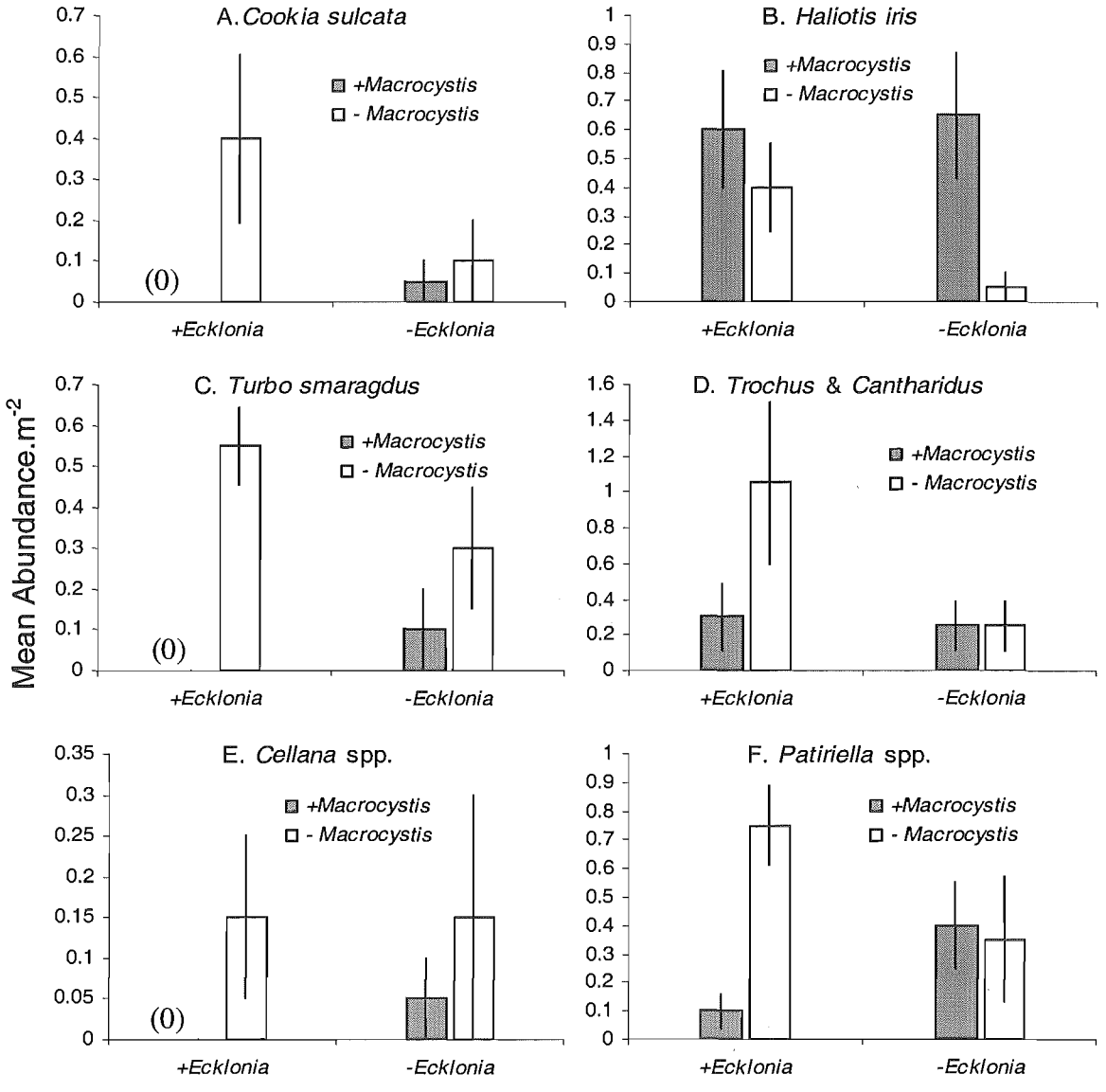

Figure 52 A-F. Mean abundance of invertebrates within canopy removal experiment ± 1SE.

The trochids, *Trochus* and *Cantharidus,* and the limpet *Cellana*, did not display any significant response to canopy removal (Figure 52d-e, Table 44, Table 45). The abundance of *Patiriella* was significantly greater when *Macrocystis* had been removed, but only when *Ecklonia* was left intact, leading to a significant interaction (Figure 52f, Table 46).

Table 41. Abundance of *Cookia sulcata*

Source	df	MS	F	P
Macrocystis Canopy	1	0.134	3.169	0.095
Ecklonia Canopy	1	0.038	0.899	0.357
Macrocystis x *Ecklonia*	1	0.138	2.325	0.091
Error	15	0.042		

Table 42. Abundance of *Haliotis iris*

Source	df	MS	F	P
Macrocystis Canopy	1	0.285	4.663	0.047*
Ecklonia Canopy	1	0.204	3.349	0.087
Macrocystis x *Ecklonia*	1	0.167	2.728	0.119
Error	15	0.061		

Table 43. Abundance of *Turbo smaragdus*

Source	df	MS	F	P
Macrocystis Canopy	1	0.326	9.010	0.009**
Ecklonia Canopy	1	0.014	0.390	0.541
Macrocystis x *Ecklonia*	1	0.076	2.092	0.169
Error	15	0.036		

Table 44. Abundance of *Trochus viridus* & *Cantharidus purpurea*

Source	df	MS	F	P
Macrocystis Canopy	1	0.126	1.297	0.271
Ecklonia Canopy	1	0.158	1.634	0.219
Macrocystis x *Ecklonia*	1	0.126	1.297	0.271
Error	15	0.097		

Table 45. Abundance of *Cellana* spp.

Source	df	MS	F	P
Macrocystis Canopy	1	0.058	1.665	0.215
Ecklonia Canopy	1	0.000	0.022	0.883
Macrocystis x *Ecklonia*	1	0.011	0.325	0.576
Error	15	0.035		

Table 46. Abundance of *Patiriella* spp.

Source	df	MS	F	P
Macrocystis Canopy	1	0.298	5.468	0.031*
Ecklonia Canopy	1	0.037	0.603	0.449
Macrocystis x *Ecklonia*	1	0.535	10.18	0.006**
Error	15	0.025		

Table 41 -Table 46. Ancova results for mean abundance of large macroinvertebrates within canopy clearance treatments. Treatments were ±*M. pyrifera* canopy, ±*E. radiata* canopy. Covariate was initial abundance. Analysis performed on log transformed data.

5.3.3 Exclusion of Grazers from Primary Substrate

No macroalgae were ever observed on any of the caged slabs deployed in Wainui Bay. There was a propensity for slabs in caged treatments to have a thicker layer of fine sediment than uncaged treatments, but this was not quantified as sediment was removed when slabs were examined. Subsequent samples until spring 1998 showed a progressive increase in the cover of a black biofilm and encrusting coralline on all slabs.

5.3.4 Exclusion/Inclusion of Cookia sulcata

5.3.4.1 Recruitment of Macroalgae

The presence or absence of *Cookia* within cages significantly affected the number of newly recruited laminarians within treatments (Table 47, Figure 53).

Table 47. Result of two-way Anova on abundance of juvenile laminarians. Treatment (+/-*Cookia*, Control) was a fixed factor, time was set as random. The first sampling date was left out of the analysis. Data were square root transformed prior to analysis.

Source	df	MS	F	p
Treatment	2	2.53	96.7	0.0004**
Time	2	0.55	1.94	0.172
Treatment x Time	4	0.26	0.09	0.984
Error	18	0.29		

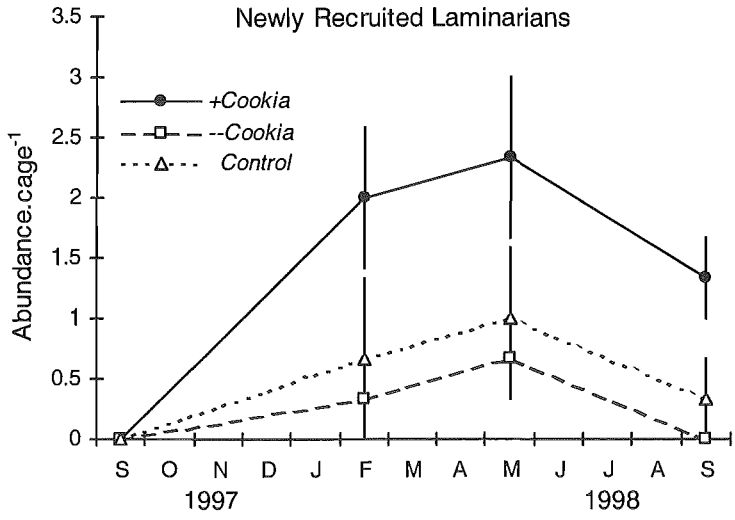

Figure 53. The abundance of newly recruited laminarian algae within cages ± 1SE. +*Cookia* = inclusion of *Cookia*, -*Cookia* = exclusion of *Cookia*, Control = cage without sides.

Laminarian recruits were significantly more abundant within the *Cookia* inclusion treatment than in either the *Cookia* exclusion treatment or the control (Tukey's HSD test <.05). Recruits generally became more abundant in all treatments from September 1997 to May 1998, but had declined in abundance in all treatments by September 1998.

Consequently, within *Cookia* inclusion treatments the abundance of juvenile *Ecklonia* became significantly more abundant (Table 48, Figure 54).

Table 48. Result of two-way Anova on abundance of juvenile *E. radiata* (<250mm). Treatment (+/-*Cookia*, Control) was a fixed factor, time was set as random. The first sampling date was left out of the analysis. Data were square root transformed prior to analysis.

Source	df	MS	F	p
Treatment	2	4.23	53.1	0.013*
Time	2	0.25	0.91	0.421
Treatment x Time	4	0.08	0.29	0.881
Error	18	0.28		

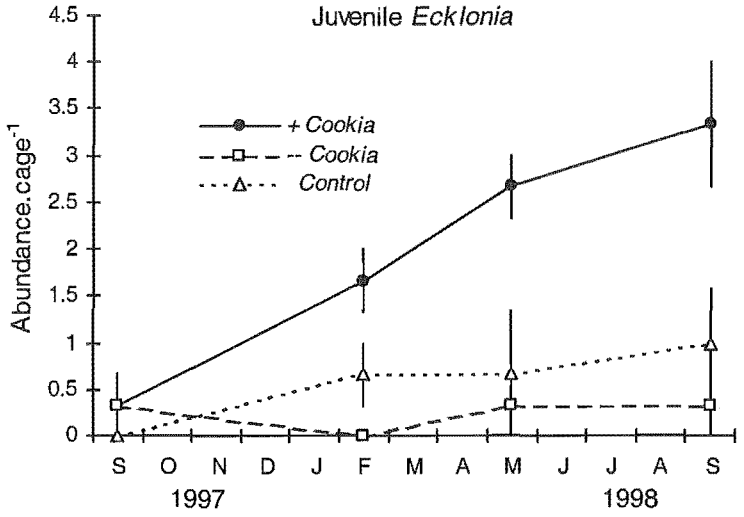

Figure 54. The abundance of juvenile *E. radiata* (<250mm) within cages ± 1SE. +*Cookia* = inclusion of *Cookia*, -*Cookia* = exclusion of *Cookia*, Control = cage without sides.

Recruitment of the fucalean alga *Carpophyllum maschalocarpum* was not significantly affected by *Cookia* caging treatment (Table 49, Figure 55). *Carpophyllum* tended to become more abundant within treatments during May 1997 (winter), but this was not significant and unrelated to the effect of treatment.

Table 49. Result of two-way Anova on abundance of *Carpophyllum*. Treatment (+/-*Cookia*, Control) was a fixed factor, time was set as random. The first sampling date was left out of the analysis. Data were square root transformed prior to analysis.

Source	df	MS	F	p
Treatment	2	0.20	0.31	0.750
Time	2	1.98	3.23	0.063
Treatment x Time	4	0.65	1.05	0.407
Error	18	0.61		

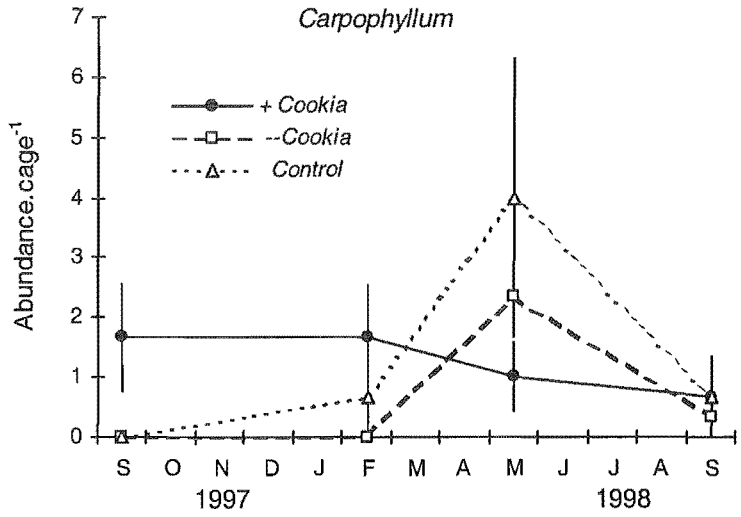

Figure 55. The abundance of newly recruited *Carpophyllum* within cages ± 1SE. *+Cookia* = inclusion of *Cookia*, *-Cookia* = exclusion of *Cookia*, Control = cage without sides.

5.3.4.2 Other Motile Organisms

The abundance of other invertebrates did not differ significantly between caging treatments. These species were *Patiriella* spp. ($F_{(2,33)}$=2.71; p=.08), Trochids (*Cantharidus purpurea & Trochus viridus*) ($F_{(2,33)}$=.484; p=.62), *Turbo smaragdus* ($F_{(2,33)}$=.350; p=.71), and *Cellana* spp.($F_{(2,33)}$=.837; p=.44). *Haliotis iris* and *Evechinus* were present in the general area but none were ever found within cages or the control. Grazing fish species *Notolabrus* spp., *Parika scaber*, *Odax pullus*, and *Forsterygion* spp. were often observed near cages, but their abundance was not recorded as these species are generally attracted by diving activity.

5.3.4.3 Sediment

There was a significant effect of *Cookia* abundance on percent cover of sediment (Figure 56, Table 50). Sediment declined slightly within inclusion cages over the first interval and remained more or less constant thereafter. The control and the exclusion cages demonstrated an increase in sediment cover from ~40% in September 1997 to ~60% in February 1998. Thereafter, sediment levels remained at ~60% in the control and the exclusion.

Table 50. Result of two-way Anova on percent cover of sediment. Treatment (+/-*Cookia*, Control) was a fixed factor, time was set as random. The first sampling date was left out of the analysis. Data were arc-sine transformed prior to analysis.

Source	df	MS	F	P
Treatment	2	581.4	43.45	0.0019**
Time	2	20.68	0.718	0.5013
Treatment x Time	4	13.38	0.464	0.7612
Error	18	28.82		

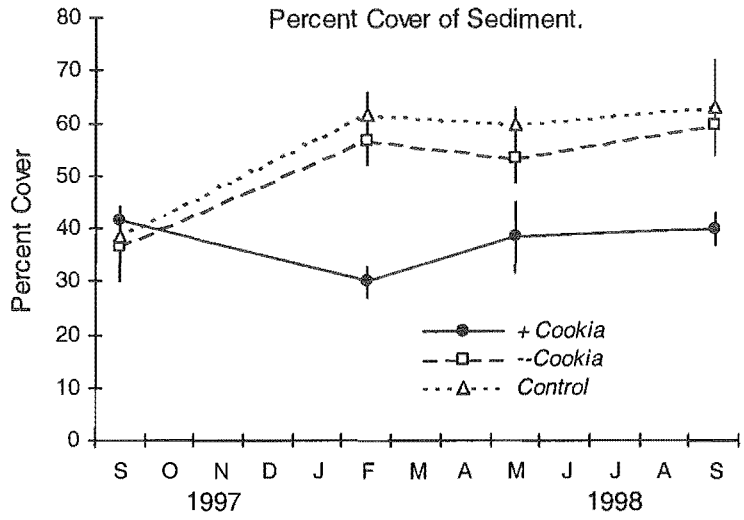

Figure 56. Percentage cover of sediment within *Cookia* cages within cages ± 1SE. +*Cookia* = inclusion of *Cookia*, -*Cookia* = exclusion of *Cookia*, Control = cage without sides.

To investigate if *Cookia* actively consumed sediment, seven large *Cookia* (70-80 mm Ø) were collected from the kelp forest, removed from their shells and preserved in 5% formalin in seawater. Stomach contents were later dissected and found to contain large amounts of sediment in addition to fragments of macroalgae, and articulated and encrusting corallines.

5.4 Discussion

The abundance of herbivorous invertebrates displayed considerable variation throughout all sites in this study. The site in Tory Channel was particularly distinct; with a generally depauperate molluscan community (Figure 51). This absence is potentially related to hydrographic and phytographic differences between these two regions. The chief difference is that Akaroa Harbour is extremely turbid in comparison to Tory Channel. Futhermore, Tory Channel has a diverse turfing algal community that is absent from Akaroa Harbour (Chapter 3). Previous studies in northern New Zealand have demonstrated that herbivorous molluscs, such as *Cookia* and *Cellana*, cannot graze effectively when a turfing algal community is present (Ayling, 1981), hence there is a strong correlation in subtidal regions of northern New Zealand between the abundance of urchins (which graze on the algal turf), and the abundance of herbivorous gastropods (which graze on areas denuded by urchins). However, urchins were conspicuously absent from all my sites, and are unlikely to be responsible for the lack of turfing algae in Akaroa Harbour. An alternate hypothesis that requires testing is that the high levels of turbidity and sedimentation within Akaroa prevent the development of a turfing community, and allows molluscan grazers to flourish. Choat & Andrew (1986) have also suggested that inhibition of turfs by deep shade or gravel abrasion may also allow subtidal herbivorous gastropods to flourish.

The effect of macroalgal canopy removal on invertebrate grazers was species specific. The three species that displayed a significant effect with canopy removal, *Haliotis*, *Turbo*, and *Patiriella*, differed markedly in their responses. The lower *Haliotis* abundance in *Macrocystis* removal treatments may be a response to disturbance and/or a change in the abundance of drift algae on which *Haliotis* feeds (Schiel *et al*, 1995). The higher abundances of *Turbo* and *Patiriella* in canopy removal treatments may be related to increased light levels within treatments, and subsequently higher levels of microalgae. The lack of response to canopy removal in *Cellana* may reflect the utilisation of distinct home sites in this species. The lack of response in *Cookia*, *Cantharidus,* and *Trochus* may indicate that these species are relatively oblivious to small-scale variation in canopy cover. In this respect, the overall impact of canopy removal on the assemblage of understorey macroinvertebrates is probably minor. The small 2 x 2m canopy 'disturbances' I performed are unlikely to have affected survival in any of the organisms examined. The effects of larger scale disturbances have been examined elsewhere (e.g. Ebeling *et al*, 1985), and have resulted in major changes in community structure.

An unexpected result of this study was that the inclusion of *Cookia* within cages appeared to enhance the recruitment and growth of macroalgae. This phenomenon is probably related to the lower levels of sediment observed within inclusion treatments, which in turn is likely to be the result of direct consumption or redistribution of sediment by *Cookia*. There may be several processes occurring within cages to bring this about. For example, cages were not insurmountable; *Cookia* numbers within cages had to be replenished at regular intervals. The exodus of *Cookia* is a likely mechanism for the net removal of sediment from inclusion cages. It is unclear why *Cookia* did not graze the recruits appearing within cages; my examination of stomach contents revealed fragments of macroalgae, and Schiel (1981) demonstrated that *Cookia* are very capable of consuming macroalgae. Nevertheless, Schiel (1981) also found little evidence to suggest that *Cookia* consumed laminarian recruits once they became visible, but probably feed on recently settled algal spores. Grazing invertebrates typically move only when feeding or looking for food (Chapman & Underwood, 1992). Thus, the departure of *Cookia* from cages may indicate that resources within cages were insufficient or were soon depleted. Laminarian recruits may have been overlooked as food items because they occurred at low densities, typically less than 2 per cage. Additionally, once these recruits grew to a size larger than could be readily consumed or disturbed by *Cookia*, cages could be beneficial to algal development, providing nutrient enrichment from *Cookia* excretion (Connor & Quinn, 1984), reduced sediment, and protection from water motion or grazing fish.

Laminarian recruitment is notoriously patchy (Kirkman, 1981; Reed 1990b; Vadas *et al*, 1992), and their absence from small-scale grazer exclusion cages may reflect this. However, it was anticipated that species of ephemeral algae, such as *Ulva* spp. or *Enteromorpha* spp, would readily colonise primary substrate in the absence of grazers. Sediment deposition combined with shading by cages could be responsible for their absence. Kennelly (1991) found that light levels were reduced by 30-60% in small (0.3 x 0.3 x 0.1m) cages, and by 10-20% in large (2 x 2 x 0.45m) cages. Water flow was reduced by 15% and 5% respectively, allowing sediment to settle more readily. Similar artefacts are likely to have occurred in the cages of my study.

This study has demonstrated that the relationship between the herbivorous invertebrates and the macroalgal community that they occupy is intractable. However, sediment may play an important role in mediating the effects of grazers on algal recruits.

Chapter 6: General Discussion

6.1 General Discussion

In this thesis I examined the demography of *Ecklonia radiata* near the limit of its range in southern New Zealand. These populations of *Ecklonia* are unique in that their occurrence is shallow, yet their light environment is generally poor, mainly as a result of high turbidity and the presence of a *Macrocystis* canopy. At a fundamental level, the persistence of *Ecklonia* in the low-light, turbid environment of Akaroa Harbour is determined by features of its life history (**Figure 57**); the response of *Ecklonia* to the physical and biological characteristics of Akaroa Harbour is simply an extension of the plasticity exhibited by *Ecklonia* over its wide geographic range (Table 3).

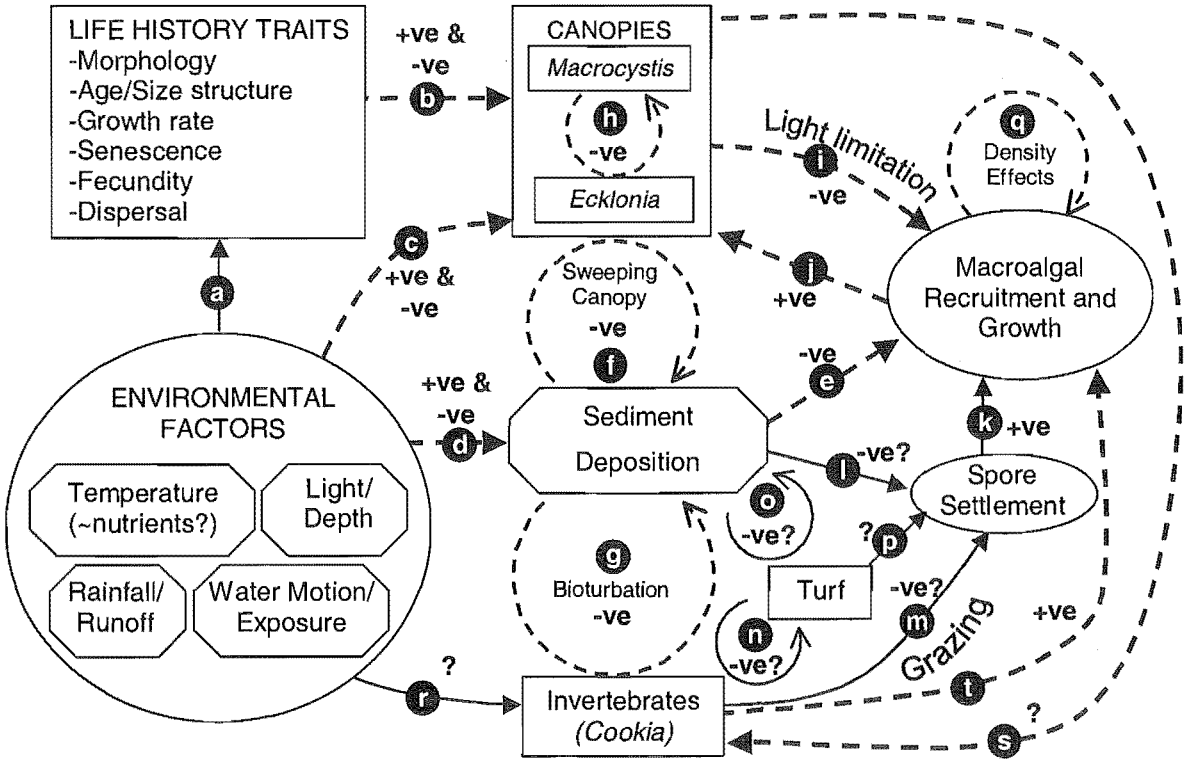

Figure 57. A hypothetical model representing the relationship between hydrodynamic processes, life-history characteristics, and biotic/abiotic interactions influencing *Ecklonia* populations in Akaroa Harbour. Dashed lines represent relationships addressed in this study. At a large scale, interactions between environmental factors and species' life history characteristics determine whether species are able to grow and persist (a, b, c). Rainfall/runoff and water motion cause the deposition and resuspension of sediment (d), which subsequently has deleterious effects on recruitment and growth of macroalgae (e). Additionally, macroalgal canopies and large invertebrates may also act to redistribute sediment (f, g). *Macrocystis* canopies suppress the growth of understorey *Ecklonia* canopies (h), and both of these canopies subsequently limit their own recruitment (i), but recruits are able to take advantage of gaps in the canopy (j). Factors affecting spore settlement and subsequent transition to recruits (k) remain obscure, but are likely to involve sediment deposition (l) and the potentially confounding effects of grazing invertebrates (m). An investigation of the lack of turfing algae may reveal interactions between invertebrates, sediment, and macroalgae (n, o, p). Intraspecific density effects are present but their effect is likely to be minor due to low recruitment densities (q). Environmental factors affecting invertebrate abundance remain obscure (r). There are significant linkages between macroalgal canopies and major invertebrate grazers (s), although these are not clear-cut and require more investigation. Additionally, in some circumstances macroinvertebrates may enhance macroalgal recruitment and growth (t).

The southern New Zealand populations of *Ecklonia* that I examined were morphologically distinct from *Ecklonia* populations in northern New Zealand and Australia (Figure 19). This extensive regional differentiation is probably related to a suite of environmental factors that vary and covary over its range. Among these, temperature, light, and daylength are likely to be important at larger scales, while vagaries of water motion, depth, turbidity, and nutrients may be quite site specific. In my study there was a broad correlative trend between stipe length and water motion, similar to that described for many other kelps (Chapman, 1973; Gerard & Mann, 1973; Mann, 1971). As discussed in Chapter 2, this may reflect either a difference in stipe allocation or a difference in size-specific mortality, or both.

Ecklonia grows poorly in Akaroa Harbour in comparison to populations elsewhere (Novaczek, 1984c; Kirkman, 1989). This may be due to a number of factors, such as light reduction by the *Macrocystis* canopy, water turbidity, nutrient limitation, and low temperatures. The low growth of *Ecklonia* is likely to have a profound influence on other life history traits. For example, *Ecklonia* did not become reproductive until they reached a size of 120-160g. Low growth rates meant that plants were unlikely to reach reproductive size until late in their second year. This delayed reproduction may only be possible because the environment is relatively benign towards *Ecklonia*; mortality is generally low, and *Ecklonia* may live to greater than 7 years. Hatcher *et al* (1987) described a population of *E. radiata* with a different 'strategy' near the northern limit of its range in Western Australia. There, plants suffered 92% mortality per year, effectively developing an annual life-history in response to harsh conditions. *Ecklonia* is iteroparous, and produces a multitude of spores, possibly at little cost (Reed *et al*, 1992). Akaroa Harbour populations of *Ecklonia* bore fertile sori year-round, although there is evidence of greater reproductive allocation during autumn and winter (Figure 13). The persistence of sori year-round may be a reflection of low lamina growth, but may also enable *Ecklonia* to take advantage of unpredictable gaps in the canopy (Reed *et al.* 1996).

Despite their long reproductive life and high fecundity, these populations of *Ecklonia* appear to be limited by recruitment. *Ecklonia* in Akaroa Harbour never obtain the high densities observed at other locations in northern New Zealand and Australia; mature plants are generally found at densities of ~4.m^{-2}, and recruits at mean annual densities of <0.5.m^{-2}. This suggests that only a very small fraction of released spores result in visible sporophytes. Chapman (1984) estimated that only 0.0002-0.00001% of kelp settlers become visible as recruits and this figure is likely to be similar in *Ecklonia*. In situ studies of pre-visible stages

of laminarians are rare (Neushul *et al*, 1976; Kennelly & Underwood, 1993), and explanations of mortality among these stages are generally speculative. In my study, inhibition by encrusting coralline algae is unlikely to be responsible for the low recruitment observed (Chapter 3) (Reed & Foster, 1984) although spore deposition onto *Litholamnion* sp. may not be favoured due to its lack of rugosity.

The large amount of sediment in Akaroa Harbour is likely to affect settlement (Devinny & Volse, 1978; Vadas *et al*, 1992; Konar & Roberts, 1996), but the nature of this effect is unclear. Kennelly (1983) has suggested that a thin layer of sediment may be beneficial to early post-settlement stages by supplying nutrients and protection. Similarly, Neushul *et al* (1976) were unable to demonstrate any detrimental effects on survival and recruitment of early post-settlement *M. pyrifera* due to sediment. In my study, the increased sedimentation in cleared areas (Chapter 3) did not appear to affect newly recruited *Ecklonia* the same way it affected juvenile growth. However, high sedimentation may indirectly support a community of grazing invertebrates, by inhibiting the formation of algal turfs (Jenkins *et al*, 1999c). These grazers may, in turn, consume algal sporelings and recruits. Here, though, the effect of grazers was confounded by their interactive effects with sediment (Chapter 5), such that it was impossible to determine if *Cookia* had a detrimental effect (by consuming recruits) or a beneficial effect (by removing sediment). Although not detritivorous, *Cookia* does consume large quantities of sediment as an incidental by-product of its normal feeding and movement behaviour. In this respect *Cookia,* to some extent, may make the environment more suitable for the growth of diatoms and sporelings on which it feeds. The clarification of potential interactions between grazers, sediment, and turfs and their effects on macroalgal recruitment will require the use of clever manipulative designs that can control for sediment and artefacts of caging.

Ecklonia recruitment is unlikely to be limited by the effects of intraspecific density between recruits. The dense aggregations of juvenile *Ecklonia* that I observed did not correspond with many models commonly used in terrestrial and marine systems, and there is little evidence that observed patterns were the outcome of density dependent effects among microscopic stages (Chapter 4). However, precursors to density effects were suggested by the results. These processes may become important at larger sizes as even-aged stands develop. Generally however, plants did not recruit in high enough densities for these effects to predominate.

Intraspecific interactions among *Ecklonia* are probably limited to the suppression of recruits by mature canopies. The most likely mechanism for this is shading; new recruits may be especially sensitive to low light levels during winter, and when surface canopies are thickest, because they lack substantial reserves of mannitol and laminarin. Thus successful recruitment of *Ecklonia* may be dependent on physical processes that affect the persistence of the macroalgal canopies. *Macrocystis* and *Ecklonia* canopies differ in their sensitivity to hydrodynamic events, and this is a reflection of their differing life-history characteristics. Canopy forming *Macrocystis* are large and physically dominate their environment, but individual plants are relatively short lived, suffering high mortality due to winter storms. Additionally, the biomass of *Macrocystis* in New Zealand declines significantly during summer due to canopy senescence (Brown *et al*, 1997). This phenomena was observed in Akaroa Harbour, especially the forests in and around Wainui Bay, where the surface canopy often disappeared completely during warmer months (Figure 3). These processes represent an immense turnover of space (and thus light) on a relatively short time scale. In contrast, *Ecklonia*, once they mature, are less prone to removal by water motion and other exogenous mortality factors such as grazers. Consequently, the *Ecklonia* subcanopy is very persistent; individual plants may occupy space for up to seven years. This suggests that fluctuations in the *Ecklonia* subcanopy may have an overriding impact on macroalgal recruitment in the face of short-term fluctuations in the *Macrocystis* canopy .

The coexistence of *Macrocystis* with other understorey species such as *Pterygophora* has been attributed to differences in life history characteristics (Reed & Foster, 1984). Similar differences in life-history traits between *Macrocystis* and *Ecklonia* may also allow them to coexist in southern New Zealand. *Ecklonia* can outlast *Macrocystis* via stress tolerance and longevity. Furthermore, even though *Macrocystis* can competitively dominate space and light, *Ecklonia* can rapidly respond to light gap opportunities. When disturbance is incorporated into this concept, differences in how the species respond suggest aspects of the intermediate disturbance hypothesis (Dial & Roughgarden, 1998; Connell, 1978). High levels of disturbance will favour subcanopy *Ecklonia*, whereas low levels of disturbance will favour *Macrocystis*. At intermediate levels of disturbance, coexistence is favoured. Similarly, Dayton *et al* (1992) found that after 2.5 years of continual removal (i.e. disturbance) of *Macrocystis* canopies, subcanopy *Pterygophora* became sufficiently dense to inhibit further *Macrocystis* recruitment. The persistence of *Pterygophora* was thus related to the frequency with which the *Macrocystis* canopy was disturbed. The persistence of *Macrocystis* in

California is dependent on low levels of disturbance; Graham *et al* (1997) measured recruitment, holdfast growth and mortality of *Macrocystis* at three sites along a wave exposure gradient. Mortality and canopy loss were greatest at the more exposed site. Recruitment patterns also varied with exposure. At the protected site, recruitment was low and continuous and there was a continuous population of juveniles. At the intermediate and exposed sites, recruitment was episodic, occurring when canopy was removed. Similarly, Van Tussenbroek (1993) has suggested that the general absence of winter storms in the Falklands Islands is responsible for the stability of *Macrocystis* forests in that area.

Kirkman (1981) has suggested that the growth pattern of *Ecklonia* in Western Australia fits into the other extreme of Connell's (1978) hypothesis. Diversity in this community is low, disturbances occur infrequently and only allow the shade tolerant subcanopy *Ecklonia* to replace lost canopy individuals. Larger disturbances in which several square meters are cleared allows other less shade-tolerant species such as *Sargassum* sp. to invade. Clearly, the relationship of *Ecklonia* to disturbance is context dependent, changing over its geographic range, and in relation to what other species are present.

The key findings of this study can be summarised as interactions between biotic and abiotic factors (Figure 57). The ecology of *Ecklonia radiata* in southern New Zealand may be affected by site-specific environmental factors, which influence demographic parameters and interactions with co-occurring biota. On a wider scale, the results of this study reflect general patterns observed in homologous communities overseas, such as the suppression of recruitment and growth by mature canopies, and responses to disturbance.

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